

MORPHOLOGICAL, FUNCTIONAL, AND EVOLUTIONARY ASPECTS OF THE FLOWER IN THE APOCYNACEAE

INAUGURAL - DISSERTATION

zur
Erlangung der Philosophischen Doktorwürde
vorgelegt der
PHILOSOPHISCHEN FAKULTÄT II
der
UNIVERSITÄT ZÜRICH

von
MARY E. FALLEN
aus U.S.A.

Begutachtet von Herrn
Prof. Dr. P.K. Endress

ADAG Administration & Druck AG

Zürich 1983



MORPHOLOGICAL, FUNCTIONAL, AND EVOLUTIONARY ASPECTS OF THE FLOWER IN THE APOCYNACEAE

INAUGURAL - DISSERTATION

zur
Erlangung der Philosophischen Doktorwürde
vorgelegt der
PHILOSOPHISCHEN FAKULTÄT II
der
UNIVERSITÄT ZÜRICH

von
MARY E. FALLEN
aus U.S.A.

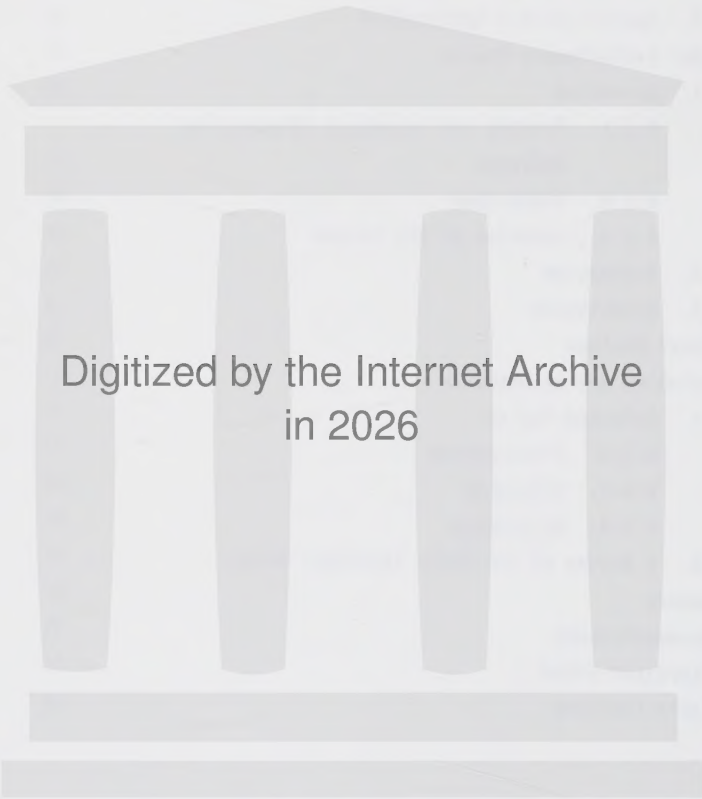
Begutachtet von Herrn
Prof. Dr. P.K. Endress

ADAG Administration & Druck AG

Zürich 1983

TABLE OF CONTENTS

	Page
Acknowledgements	5
1. Introduction	6
2. Materials and Methods	7
3. Selected Species Descriptions	11
3.1. Species without a Gynostegium	11
3.2. Species with a Gynostegium	19
4. Major Evolutionary Trends	25
4.1. Gynoecium	25
4.1.1. Primary and Secondary Syncarpy and Apocarpy	25
4.1.2. Style-head	28
4.1.3. Location of the Stigma	30
4.2. Androeceum	31
4.3. Gynostegium	34
5. Floral Biology	35
6. Evolution and Systematics	37
6.1. Selected Topics	37
6.1.1. Pleiocarpeae	37
6.1.2. <u>Allamanda</u>	40
6.1.3. <u>Holarrhena</u>	42
6.2. A Survey of the Major Taxonomic Groups	44
7. Summary	49
8. Zusammenfassung	51
9. Literature Cited	53
10. Figure Captions	59



Digitized by the Internet Archive
in 2026

Acknowledgements.

I thank Prof. Peter K. Endress for his advice and support throughout the study and Prof. Friedrich Markgraf for helpful suggestions. I also thank Prof. Manfred Hesse for stimulating discussions on alkaloid chemistry and for allowing me to use as yet unpublished data. Special thanks go to the many people who have provided FAA-fixed material, in particular, Prof. A.J.M. Leeuwenberg and Valerio Fletchmann Ferreira. I am grateful to the Directors of the Institut für Systematische Botanik and the Institut für Pflanzenbiologie der Universität Zürich for use of the facilities, and to Mr. U. Jauch for technical assistance with SEM preparations. Some of the specimens investigated were collected by Prof. P.K. Endress during travel supported by the Georges-und-Antoine-Claraz-Schenkung, which is also gratefully acknowledged.

Introduction.

The Apocynaceae is a large, diverse, predominantly tropical plant family, with an extremely complex floral structure. For many genera the only information available is of a descriptive nature, often compiled from herbarium material. Functional aspects of the floral structure have been considered by: Sprengel (1793), Delpino (1867), Ludwig (1880), French (1883), Frye & Blodgett (1905), Church (1908), Demeter (1922), Boke (1948, 1949), Safwat (1962), Allorge (1976), Walker, (1975, 1978), Rowley (1980), Schick (1980, 1982), Endress et al. (in press), but for the great majority of genera it remains unknown.

The present comparative study on the floral structure of representatives of the four subfamilies of the Apocynaceae was undertaken to better understand the structure and function of little known groups, to find new aspects of evolutionary trends, and to contribute toward a better classification of the higher taxa of the family.

2. Materials and Methods.

Flowers of the following collections were used for this study. Specimens lacking a collector number are identified by their number in my section series and are preceded by F-. In all cases where herbarium material was used, flowers were removed from sheets deposited in the herbarium at the Botanischer Garten der Universität Zürich (Z).

Material fixed in FAA:

Apocynaceae

Acokanthera oppositifolia (Lam.) Codd, Fallen s.n., F-591-613, cultivated, Botanischer Garten der Universität Zürich, Switzerland.

Adenium oleifolium Stapf, Fallen s.n., F-1689-1722, cultivated, Städtische Sukkulanten-Sammlung Zürich, Switzerland.

Agonosma dichotoma (Roth) K. Schum., Thanikaimoni 1759, India.

Alafia barteri Oliv., Leeuwenberg 12156, Africa.

Allamanda schottii Pohl, Fallen s.n., F-427-472; F-1846-1878, cultivated, Botanischer Garten der Universität Zürich, Switzerland.

Alstonia viellardii v. Heurck & Müll.-Arg., Endress 6205, New Caledonia.

Alyxia clusiophylla (Baillon) Guillaumin, Endress 6237, New Caledonia.

Alyxia olivaeformis Gaudich., Neill 5290, Hawaii.

Ambelania grandiflora Huber, Ferreira s.n., F-2061-2079; F-2105-2123, cultivated, Jardim Botânico, Rio de Janeiro, Brazil.

Ancyclobotrys scandens (Schum. & Thonn.) Pichon, Breteler 2882, Africa.

Aphanostylis mannii (Stapf) Pierre, Leeuwenberg 9065, Africa.

Apocynum androsaemifolium L., without name of collector, F-311-325; F-1476-1481, cultivated, Botanischer Garten, St. Gallen, Switzerland.

Apocynum cannabinum L., Dorr 2385, Oklahoma, U.S.A.

Artia balansae (Baillon) Pichon, McPherson 5063, New Caledonia.

Aspidosperma pyricollum Müll.-Arg., Ferreira s.n., F-793-800, cultivated, Jardim Botânico, Rio de Janeiro, Brazil.

Baissea multiflora A. DC., De Kruif 675, Africa.

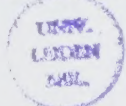
Beaumontia grandiflora Wall., Endress 6004, cultivated, new Botanical Garden, Brisbane, Australia.

Callichilia barteri Stapf, without name of collector, F-1218-1263, Africa.

Catharanthus roseus (L.) G. Don, cultivated, Botanischer Garten der Universität Zürich, Switzerland.

Cerbera manghas L., Endress 6283, New Caledonia.

Cerberiopsis neriifolia (S. Moore) Boiteau, McPherson s.n., F-1992-2014, New Caledonia.



Cerberiopsis obtusifolia (v. Heurck & Müll.) Boiteau, Endress 6416, cultivated, new Botanical Garden, Brisbane, Australia.

Cleghornia cymosa Wight, Burck 343, Sri Lanka.

Condylocarpon guyanense Desf., Sastre 5470, French Guiana.

Forsteronia acouci (Aubl.) A. DC., Zarucchi 1665, Colombia.

Funtumia africana (Benth.) Stapf, Zwetsloot 5, Africa.

Funtumia elastica (Preuss) Stapf, Leeuwenberg 11072, Africa.

Geissospermum laeve (Vell.) Miers, Ferreira s.n., F-783-792, Brazil.

Haplophyton crooksii L. Benson, Gilbertson s.n., F-1646-1654, Arizona, U.S.A.

Holarrhena floribunda (G. Don) Dur. & Schinz, Leeuwenberg 9664, Africa.

Holarrhena mitis (Vahl.) R. Br., Leeuwenberg 10709, Africa (cultivated).

Holarrhena pubescens (Buch.-Ham.) Wall. ex G. Don, Leeuwenberg 10867, Africa.

Isonema smeathmannii R. & S., without name of collector, F-1146-1162, Africa.

Kopsia fruticosa A. DC., Prévost 167, Java.

Landolphia owariensis Beauv., Breteler & De Wild 627, Africa.

Mandevilla laxa (R. & P.) Woods., Jenny s.n., F-878-906; F-958-978, cultivated, Isole di Brissago, Switzerland.

Mandevilla sanderi (Hemsl.) Woods., Fallen s.n., F-1951-1961, cultivated, Royal Botanic Gardens, Kew, England.

Melodinus balansae Baillon, Endress 6034, New Caledonia.

Mortoniella pittieri Woods., Stevens 3663, Nicaragua.

Motandra guianensis A. DC., Breteler 1207, Africa.

Neisosperma nakaiana (Koidz.) Fosberg & Sachet, Neill 5291, Hawaii.

Nerium oleander L., Fallen s.n., F-1295-1331, cultivated, Botanischer Garten, Zürich, Switzerland.

Oncinotis pontyi Dubard, De Konig 4796, Africa.

Pachypodium baronii Costantin & Bois var. Windsor, without name of collector, F-1723-1747, cultivated, Städtische Sukkulenten-Sammlung, Zürich, Switzerland.

Pachypodium lamerei Drake, without name of collector, F-1078-1132; F-1482-1564, cultivated, Städtische Sukkulenten-Sammlung, Zürich, Switzerland.

Parsonsia capsularis (G. Foster) R. Br., Endress 6385, New Zealand.

Parsonsia straminea F. Müll., without name of collector, F-760-782; F-1363-1378, cultivated, Botanical Garden Canberra, Australia; living plant number CAN-740099.

- Peschiera australis (Müll.-Arg.) Miers, Ferreira s.n., F-1379-1401, cultivated, Jardim Botânico, Rio de Janeiro, Brazil.
- Picralima nitida (Stapf) Th. & H. Dur., Assi s.n., F-1009-1024, Ivory Coast, Africa.
- Picralima nitida (Stapf) Th. & H. Dur., Leeuwenberg 10779, Africa.
- Pleiocarpa mutica Benth., van Setten 415, Africa.
- Pleioceras barteri Baillon, Assi s.n., F-913-921, Ivory Coast, Africa.
- Plumeria rubra (Ait.) Woods., Fallen s.n., F-816-827, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Plumeria rubra (Ait.) Woods., Jenny s.n., F-807-815, cultivated, Isole di Brissago, Switzerland.
- Prestonia riedelii (Müll.-Arg.) Mgf., Ferreira s.n., F-1171-1211, São Paulo, Brazil.
- Rauvolfia balansae (Baillon) Boiteau, Endress 6279, New Caledonia.
- Rauvolfia reflexa Teijsm. & Binn., Ferreira s.n., F-801-803, cultivated, Jardim Botânico, Rio de Janeiro, Brazil.
- Rauvolfia sandwicensis A. DC., Neill 5269, Hawaii.
- Rhazya orientalis A. DC., Fallen s.n., F-1402-1414, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Saba florida (Benth.) Bullock, Leeuwenberg 12249, Africa.
- Stephanostema stenocarpa Schum., Fallen s.n., F-1349-1362, cultivated, Royal Botanic Gardens, Kew, England.
- Strophathus divaricatus (Lour.) Hook. & Arn., Ferreira s.n., F-922-946, cultivated, Jardim Botânico, Rio de Janeiro, Brazil.
- Thevetia ahouai (L.) A. DC., Fallen s.n., F-1748-1765, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Thevetia peruviana (Pers.) Schum., Fallen s.n., F-349-401; F-1901-1938, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Trachelospermum jasminoides (Lindl.) Lem., Fallen s.n., F-402-426; F-1661-1676, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Vallaris heynii Spreng., Thanikaimoni 1760, India.
- Vinca minor L., Fallen s.n., F-500-518, Zürich, Switzerland.
- Vinca minor L., Fallen s.n., F-1655-1660, cultivated, Botanischer Garten der Universität Zürich, Switzerland.
- Voacanga africana Stapf, Leeuwenberg 9472, Africa.
- Wrightia religiosa (Teijsm. & Binn.) Benth., without name of collector, F-1677-1688, cultivated, Botanic Gardens of Indonesia, Bogor.

Asclepiadaceae

Asclepias physocarpa (E. Mey.) Schltr., Endress 6406, southern Queensland, Australia.

Cryptolepis buchananii R. & S., without name of collector, F-1896-1900, India.

Hemidesmus indicus (L.) R. Br., without name of collector, F-1842-1845, India.

Periploca graeca L., Fallen s.n., F-1428-1463, cultivated, Botanischer Garten der Universität Zürich, Switzerland.

Material from Herbarium Specimens:

Apocynaceae

Alyxia podocarpa v. Heurck & Müll.-Arg., Däniker 706, New Caledonia.

Anechites nerium (Aubl.) Urb., Asplund 16471, Ecuador.

Aspidosperma illustre (Vell.) Kuhl. & Piraja, Sucre 8348, Linhares, Brazil.

Craspidospermum verticillatum Boj. ex DC., Rensch 3602, Madagascar.

Himatanthus obovata (Mgf.) Woods., Hatschbach 37431, Minas Gerais, Brazil.

Ichnocarpus frutescens R. Br., Kramer & Nair 5942, India.

Landolphia kirkii Dyer, Swynerton 81, Africa.

Laubertia boisieri A. DC., Nuñez 6943, Peru.

Macoubea guianensis Aublet, Silva 1039, Amazonas, Brazil.

Malouetia tamariquina (Aubl.) A. DC., Anderson 10972, Brazil.

Pottsia laxiflora (Bl.) O. Ktze., Ying 685, Hong Kong.

Skytanthus martianus (Müll.-Arg.) Benth., Duarte 10508, Minas Gerais, Brazil.

Tonduzia parviflora Pittier, Tonduz 17694, Costa Rica.

Vallesia glabra Cav., Petersen 12824, Argentina.

Asclepiadaceae

Cryptolepis scandens Schers., Baum 577, S.W. Africa.

Ectadium virgatum E. Mey., De Winter 6177, S.W. Africa.

Hemidesmus indicus (L.) R. Br., Prain s.n., F-742-747, cultivated, Botanical Garden Calcutta, India.

Raphionacme burkei N.E. Br., Dinter 4348, S. Africa.

Secamone alpinii Schultes, Bayliss 3108, S. Africa.

Specimens were dehydrated in an alcohol-xylol series, embedded in paraplast, cut with a rotary microtome at 10 micrometers, and stained with safranin and astra blue. Herbarium material used in sectioning was pre-

treated by boiling 3-4 minutes, then soaking in a dilute KOH solution for one hour at 62°C to expand the tissues. Drawings were made using a Wild microscope with drawing attachment. For SEM studies material fixed in FAA was prepared by critical point drying and Au-sputtering.

3. Selected Species Descriptions.

3.1. Species without a Gynostegium:

1. Aspidosperma pyricollum. The flowers exhibit several features which are typical for a relatively primitive apocynaceous flower. The reproductive organs are completely enclosed within the corolla tube. The stamens are inserted above the level of the style-head and are free from it (Fig. 1). The anthers are neither morphologically nor histologically specialized (Fig. 2a). An important character for the genus are the gaps in the corolla tube at the level of stamen insertion (Fig. 2b). The style-head is cone-shaped. The apex contains masses of tracheids and appears nonreceptive. The remainder is covered with a secretory epithelium which has the dual function of stigma as well as adhesive production (Figs. 1, 2c). Thus, with the exception of the apex, the entire style-head appears receptive. It contains transmitting tissue that extends as a central column through the long, slender, postgenitally fused styler region (Fig. 2d) and opens up into the ovary cavity and along the placentae. The ovary is bicarpellate and apocarpous, with each carpel containing 5-6 ovules. The placentation is axile and the ovules are arranged biserially (Fig. 2e).

In the genus Aspidosperma one carpel usually aborts during development so that at maturity the fruit consists of a single, somewhat flattened, dolabriform follicle. The seeds are surrounded by a papery wing, and are wind-dispersed.

2. Pleiocarpa mutica. The floral structure is similar to that of Aspidosperma pyricollum. The anthers exhibit neither morphological nor histological modifications (Fig. 4a), there are gaps in the corolla tube behind the insertion of the staminal filaments (Fig. 4b), and the style-head is simple and cone-shaped (Fig. 3) with a secretory epithelium that functions both as stigma and in the production of adhesive. In P. mutica, however, the style-head is formed by the union of five carpel apices. The five segments are still distinguishable in the style-head (Fig. 4c) and in the styler region.

The inner parts of the carpels in the postgenitally fused region differentiate into transmitting tissue, but a solid cylinder of transmitting tissue does not form. Instead, a more or less hollow cylinder forms, with the transmitting tissue accumulating around its periphery (Fig. 4d). It is assumed that pollen tube growth is confined basically to the periphery of the hollow cylinder throughout most of the length of the style. The ovary is apocarpous, consisting of 5 carpels containing one ovule each (Fig. 4e). Placentation is axile.

In the fruiting stage the mericarps are fleshy and indehiscent. They are yellowish- to reddish-orange, and are probably dispersed by specialist frugivores (as defined by McKey, 1975).

3. Geissospermum laeve. Except for the dextrorse aestivation of the corolla lobes, the floral structure is very similar to that of Aspidosperma and Pleiocarpa, with morphologically and histologically unspecialized anthers which are not adherent to the style-head (Fig. 6a), gaps in the corolla tube at the insertion of the staminal filaments (Fig. 6b), and a simple cone-shaped style-head (Figs. 6c, 5). The ovary is made up of two carpels that are congenitally fused at the base and apocarpous above. Each carpel contains about 8 ovules arranged biserially (Fig. 6d).

The fruit consists of two fleshy mericarps. The seeds are partially embedded in a white, fleshy tissue (a funicle according to Miers, 1878). Dispersal is probably by specialist frugivores. (From the literature, I have not been able to determine whether or not the fruits are dehiscent for this genus.)

4. Haplophyton crooksii. The aestivation of the corolla lobes is dextrorse. The floral structure is similar to Aspidosperma and Geissospermum (Figs. 8a, b, c), but the style-head differs in having two large papillose apices (Fig. 7). The two carpels are apocarpous and contain about 7 ovules each (Fig. 8d).

The fruit comprises two slender, terete follicles. The seeds have a coma at both ends and are wind-dispersed.

5. Landolphia owariensis. The stamens are inserted on the corolla tube at the level corresponding to about the middle of the style-head. The anthers are simple and undifferentiated, with neither morphological nor histological modifications of the anther body. They are situated at about the level of the upper style-head and dehisce introrsely, shedding their pollen

toward the center of the flower (Fig. 10a) (presumably onto the upper style-head where it is presented). The style-head is cone-shaped and is differentiated into a non-secretory upper part (Fig. 10b) that is composed mostly of dark red-staining cells (probably tanniferous) and a lower part that is covered by a secretory epithelium (Fig. 10c). At the interface between these two regions the epidermis produces a ring of ascending hairs of only a few cell layers (Fig. 9). Although the entire lower part of the style-head appears to be uniformly secretory, only the lower two-thirds appears receptive. From this level the pollen tube transmission tissue transverses the style as a solid cylinder (Fig. 10d) and continues along the placentae. The ovary is unilocular with parietal placentation and is made up of two congenitally fused carpels, each of which contains approximately 60-75 ovules arranged in many rows (Fig. 10e).

The fruit is an indehiscent berry with a fleshy pericarp that contains a peripheral layer of sclereids. The seeds are embedded in the pulpy placenate. The ripe fruits are purplish-gray in color and are said to taste sweet and sour at the same time (Pichon, 1953a), suggesting dispersal by specialist frugivores.

6. Kopsia fruticosa. An unusual character of Kopsia is the dextrorse aestivation of the corolla lobes, a trait that is typical in the Apocynoideae, but infrequent in the Plumerioideae. As in Aspidosperma and Pleiocarpa, the anthers are unspecialized and are situated above the style-head (Figs. 12a, b). The style-head, however, shows a greater degree of differentiation (Fig. 11). The apex is mostly composed of tracheid groups and lacks a secretory epidermis. The main body of the style-head is cylindrical and is uniformly covered by a thick secretory epidermis. The cells in this region are specialized for the production of adhesive used in pollen transportation. In transverse section the adhesive appears as a dense pink-staining ring around the style-head at this level (Fig. 12c). At the base of the style-head is a membranous annulus, under which the stigmatic zone is located (Fig. 12d). The transmitting tissue begins here, where the diameter of the style-head is greatest, and forms a cylinder through the style (Fig. 12e). The ovary is apocarpous and bicarpellate. Each carpel contains two ovules, biserially arranged. Two tall, pyramidal nectaries alternate with the carpels (Fig. 12f). One ovules in each carpel deteriorates during development, resulting in a single-seeded mericarp at maturity.

In the fruiting stage each carpel has a peculiar projection on its ventral wall. These deformations of the ovary wall overlie a large cavity that develops in the thick endocarp, separate from the seed-containing part (Markgraf, 1972; Markgraf & Huber, 1975). Both the thick pericarp and the air cavity are adaptations to dispersal by sea water. This view is strengthened by the fact that the cavity is lacking in a few mainland species and is most strongly developed in those species which have the widest distribution in Malesia and the islands of the Pacific (Markgraf & Huber, 1975).

7. Neisosperma nakaiana. Neisosperma is closely related to Kopsia, and the two genera have a similar floral structure. As in Kopsia, the corolla lobes have a dextrorse aestivation. Another feature which sets Neisosperma apart from most genera of the Plumerioideae is that the anthers contain a definite region of sclerenchyma along their dorsal side (Figs. 14a, 13). The upper portion of the style-head is covered with a uniform epidermis that is specialized for the production of adhesive (Fig. 14b). Toward the base of the style-head longer papillae mark the stigmatic zone (Fig. 14c). The transmitting tissue forms an inverted cone within the style-head, and continues as a cylinder through the center of the slender style (Fig. 14d) until it reaches the ovary. The ovary is comprised of two carpels that are congenitally fused at the base (Fig. 14f), but apocarpous above (Fig. 14e). Each carpel contains 4-5 biserially arranged ovules.

The fruits are apocarpous and equipped with an extremely thick spongy or fibrous endocarp: an obvious adaptation to sea water dispersal. (The genus is restricted almost exclusively to Malesia and islands of the Pacific.)

8. Thevetia ahouai. The reproductive organs are completely included in the corolla tube. Above the stamens the corolla tube is occluded by outgrowths of the corolla tube (usually referred to as "suprastaminal appendages") that have a dense indument of hair at the margins. The sessile anthers rest on top of the style-head. The thecae dehisce sublaterally (Fig. 16a) shedding their pollen onto the broad style-head. The anthers are histologically unspecialized. Morphological modifications have, for the most part, taken place in the connective, and include the broadened base that causes the thecae to diverge to the sides of the anther at the base, and the elongate apices which converge on top of the style-head and become connate by a postgenital fusion. The style-head is roughly ovoid with a broad equatorial ring. Above the equatorial ring the style-head

slopes gradually to the blunt, slightly bilobed apex. This part is covered by the anthers for the most part and does not appear to be receptive. The equatorial ring is specialized for the production of adhesive. It is folded so that the tissue hangs down in ten lobes that act as a trap for foreign pollen. The blade-like "infrastaminal appendages" project from the corolla tube and fit into five of the grooves between the lobes, where they fuse postgenitally with the style-head (Fig. 15). These five grooves alternate with the remaining five, which appear to be the major stigmatic regions (Fig. 16b). The pollen tube transmitting tissue converges at the base of the style-head (Fig. 16c) and forms a cylinder through the style. The carpels are congenitally fused from the base for about half the length of the ovary, and are apocarpous above. Each carpel contains two laterally displaced ovules. Placentation is axile (Fig. 16d).

The fruit is almost completely syncarpous. It is drupe-like (according to Gensel (1969), the stony endocarp does not fuse between the carpels nor along the ventral slit of each carpel. Thus each individual seed is enclosed in a stony layer and surrounded by the common fibrous mesocarp). Although all four ovules may develop, it is common for one or more ovules to abort during development.

The fruits are brilliant red at maturity, which suggests dispersal by frugivorous birds. However, the fibrous, white mesocarp is reported to be an important item in the diet of capuchin monkeys in Central America (J. Saunders, pers. comm.). The fruits are usually reported to be highly poisonous, though it is probably only the seeds that are toxic. The seeds have a toothed wing.

9. Allamanda schottii. The reproductive organs are located in the lower part of the corolla tube, well below the showy, expanded yellow funnel of the upper part. They are concealed by a dense growth of long, ascending hairs that arise from the corolla tube behind the anthers. The hairs sweep up over the tops of the anthers and converge in the center, occluding the corolla tube. This not only buffers the reproductive organs from the outside environment, but also prevents access to the nectar to all but the legitimate pollinators, since only a very long, slender proboscis can push aside the soft hairs and reach the nectar at the base of the corolla tube (Fig. 17). The anthers are morphologically differentiated, with the thecae above the level of the style-head (Fig. 18a). Robust (though non-sclerenchymatous) side wings are developed which extend down to about the level of the style-head apices (Fig. 18b). The style-head apices contain masses of

tracheids. Directly below this is a wreath of long, spreading hairs (Fig. 18c). Two different kinds of secretions can be distinguished in this region. One stains very dark blue and forms a thick ring around the style-head; to the outside of this ring is a thin band of a pink-staining secretion. This zone abruptly gives way to a region of shorter hairs that uniformly cover the sides of the lower half of the style-head (Fig. 18d). These hairs produce the pink-staining secretion, which at this level encircles the style-head in a thick ring. A slight amount of the deep blue-staining secretion is still visible around the outer edge of the ring. At the base of the style-head is a membranous collar which hangs down below the style-head. The stigmatic zone is at the base of the style-head, up under this annulus (Figs. 17, 18e). From here the transmitting tissue (the compitum) extends in a cylinder through the style. The staminal filaments, although fused with the corolla tube at this level, protrude inward under the style-head (Fig. 18f). This has the effect of partitioning the corolla tube into five channels. It also causes the style-head to be broken off and borne away with the falling corolla in post-anthetic flowers. The two carpels are completely postgenitally fused. At the opening of the ovary cavity a rift appears in the median plane of the ovary, splitting the tissue along the ventral slit of the two carpels (Fig. 18g). The result is an (ontogenetically) secondarily syncarpous, unilocular ovary with parietal placentation. Each placenta bears about 7-8 ovules arranged in four series (Fig. 18h).

The fruit is a dry, septicidal capsule covered by spiny projections. The seeds are surrounded by an expanded, irregularly thickened margin. The capsule has a very low specific weight due to air trapped within the ovary cavity. In addition, the spine-like projections of the carpel wall are hollow, making the fruit quite buoyant. These are apparently adaptations for water dispersal. This view is supported by the aerodynamically inefficient "wings" of the seeds, and further by the fact that the native habitat of Allamanda is in riverine forests in north-eastern Brazil.

10. Callichilia barteri. The reproductive organs are totally included within the corolla tube. The anthers are differentiated, with the thecae restricted to the distal end, above the level of the style-head. The dorsal side of the anther is composed of sclerenchyma, making it rigid. Below the thecae this tissue develops into long, elaborated side wings that extend down below the style-head. The anthers dehisce introrsely, releasing pollen into a central chamber above the style-head. At the level of the thecae

the sclerenchymatic tissue of the anthers is restricted to a narrow band along the dorsal part of the anther (Fig. 20a). A large parenchymatous, dorsal appendage develops below the level of the thecae. In this region the anther body broadens considerably, bringing adjacent side wings into juxtaposition. The sclerenchyma is displaced into the side wings, and there is a zone of cells with thick walls that do not stain with the dyes used, between the sclerenchymatous tissue of the side wings and the parenchymatous tissue of the dorsal appendage (Fig. 20b). The style-head is covered by a secretory epidermis. The upper part is star-shaped, with five slender, acuminate lobes. Long hairs radiate outward from the lobes (Fig. 20c) and arch up over the apices of the style-head (Fig. 19). Somewhat below this the style-head is still 5-angled, but the lobes are much reduced and the epidermal cells are shorter. This is the region in which adhesive is produced. At this level the dorsal appendage of the anthers has fused with the corolla tube. Since this is below the level of the main anther body, the basal extensions of the side wings appear free-standing on either side of the tissue of the dorsal appendage in cross section (Fig. 20d). The five lobes of the style-head gradually diminish and the lower style-head is ovoid. The base of the style-head is stigmatic (Fig. 20e). The transmitting tissue forms around the edges of the more or less hollow cylinder through the stylar region. Interestingly, the style is 5-angled below a more cylindrical region (Fig. 20f). In the ovary the two carpels are congenitally fused just at the base and apocarpous above. It is surrounded at the base by a lobed nectary to which it is adnate basally. Each carpel contains about 70 ovules. Placentation is axile and the ovules are arranged in 9-10 rows (Fig. 20g). There is a layer of deep red-staining tissue (tannins?) just beneath the epidermis of the outer ovule wall.

The fruit is apocarpous, being comprised of two yellowish-orange, fleshy mericarps containing many seeds. The seeds have a very thin aril and are embedded in a fleshy pulp. The mericarps are only tardily dehiscent, supposedly after the fruit is shed (Beentje, 1978). Dispersal is probably by specialist frugivores.

11. Voacanga africana. The corolla tube is conspicuously twisted. The anthers are differentiated as in Callichilia. They differ in that they lack the dorsal outgrowth and that they are sessile. The tips of the anthers are exerted. Each anther has two vascular bundles. The tissue around the vascular bundles is parenchymatous, and the thecae walls contain the typical endo-

thelial thickenings (Fig. 22a). The sessile anthers are adnate to five thick protuberances of the corolla tube, forming a close-fitting cone around the style-head. These projections with their attached anthers subdivide the corolla tube into five chambers. The tissue in the zone where the anthers merge with the corolla tube is composed of cells with thick walls that do not stain with the dyes used. This tissue allows a certain amount of flexibility to the rigid anther cone and is probably necessary for the proper functioning of the pollination mechanism. The style-head is covered by a short-celled secretory epidermis that is interrupted at about midway by an equatorial collar-like wreath of hairs (Fig. 21). It has a 5-lobed crest at its summit. Each lobe "fits" into a broad concavity in the face of the anther. The upper half of the style-head is 5-angled and is specialized for the production of adhesive. Near the lower limit of the adhesive-producing zone the corolla tube protuberances enlarge, bringing the broad side wings of adjacent anthers very near together (Figs. 22b, c). The equatorial hair wreath marks the stigmatic region. The style-head reaches its greatest diameter here, and fits closely within the surrounding anther cone (Fig. 22d). The lower half of the style-head is cylindrical; very little secretion was seen in this region (Fig. 22e). In the styler region the corolla tube protuberances enlarge to the point where the channels between them are quite narrow, and rotate, due to the twisted corolla tube (Fig. 22f). The ovary is apocarpous except at the very base. Each carpel contains about 250 ovules. Placentation is axile and the ovules are multiseriably arranged. A nectiferous disc is present at the base of the ovary, with numerous stomata in the epidermis.

The fruit consists of two globose, fleshy mericarps, which contain numerous seeds embedded in pulpy arils. The mericarps remain closed at maturity or are only tardily dehiscent. Specialized frugivores are the suspected dispersal agents.

12. Ambelania grandiflora. The anthers are free from the style-head and are morphologically and histologically differentiated as in Voacanga, with pollen production restricted to the upper region of the anther; below this the anther body develops broad sclerenchymatous side wings that form elongate basal appendages. The anthers are sessile on five protuberances of the corolla tube (Fig. 35). As in Voacanga a region of cells (with walls that do not stain with the dyes used) develops between the sclerenchymatous tissue of the anther and the parenchymatous tissue of the corolla tube. The style-head is structurally similar to that of Callichilia and Voacanga. The upper part

forms five columns that are covered by long, pale blue-staining hairs (Fig. 36b). The main function of this region is presumably pollen presentation. Directly below this the style-head is cylindrical and is covered by a short-celled, secretory epidermis (Fig. 36c) that secretes the pink-staining pollen adhesive. The base of the style-head forms an expanded disc that is covered by long hairs. The lower half of the disc is stigmatic, with the pollen tube transmitting tissue beginning at the periphery (Fig. 36d) and gradually converging in the center at the beginning of the stylar region. The pollen tube transmitting tissue proceeds as a cylinder through the center of the style (Fig. 36e) and disperses along the placentae in the ovary. The two carpels are congenitally fused, forming a unilocular ovary with parietal placentation (Fig. 36f). Each "t-shaped" placenta produces about 60-80 ovules arranged in 7-8 series.

The fruit is an indehiscent berry. Ducke (1922) reports that at maturity the fruits are black and have a very disagreeable taste. The seeds are released as the pericarp rots. They are not surrounded by a pulp as in the Carisseae. The seed coat is thick and covered by small, corky tuberculae. This is a derived condition, and is interpreted as a shift from mammal to water dispersal. This type of adaptive shift is not uncommon in species which, like Ambelania grandiflora, occur in the inundated Amazonian "Igapó" forest (Prance & Mori, 1978; Gentry, pers. comm.).

3.2. Species with a Gynostegium:

1. Wrightia religiosa. The corolla is subrotate, and unlike most members of the Apocynoideae, in Wrightia the lobes have a sinistrorse aestivation. The stamens are inserted at the mouth of the corolla tube and are completely exerted on slender filaments. The filaments are sclerohymatous except near the base, where they expand before merging with the corolla tube (Fig. 23). The side wings of adjacent anthers are very near one another, so that the anthers form a tight-fitting cone around the style-head. They dehisce introrsely releasing their pollen into a central chamber above the style-head (Fig. 24a). They are highly elaborated and morphologically and histologically differentiated as follows. The main body of the anther is sclerenchymatous. Dorsally the broad sclerenchymatic side wings terminate in slender, attenuate basal appendages. The ventral face of the anther is divided into three distinct regions. The pollen-producing tissue is restricted to the upper part. Below this the ventral face of the anther is concave. At the base of the con-

cavity is a tuft of long, sclerified hairs. It appears that the hairs are secretory at the base, producing a clear-pinkish substance which helps attach the anthers to the style-head. This subdivides the corolla tube into five chambers at this level (Fig. 24d). The style-head also shows considerable differentiation and specialization. The two free apices and the uppermost part contain masses of tracheids and are devoid of a secretory epidermis (Fig. 23). This corresponds to the level of the anther thecae (Fig. 24b). Below this the epidermis is specialized for the production of adhesive. The pale pink-staining secretion spreads out from the style-head, filling the space between the style-head and the surrounding cone of anthers (Fig. 24c). This region corresponds to the ventral concavity of the anthers. At the level where the sclerified anther hairs intermesh with the papillae of the style-head, the blue-staining epithelium ends abruptly and is replaced by another region with shorter epithelial cells that stain blue. No appreciable amount of secretion seems to be produced by the style-head at this level. Instead, the secretion cementing the anthers to the style-head seems to emanate from the secretory bases of the sclerified anther hairs. The style-head has an abbreviated annulus at the base, under which is the stigmatic zone. The transmitting tissue lies around the periphery of a more or less hollow cylinder that passes through the center of the style (Fig. 24e) and opens into the ovary cavity. The two carpels are congenitally fused only at the very base of the ovary and apocarpous above. Each carpel contains about 50 ovules. Placentation is axile and the ovules are arranged in several rows (Fig. 24f). There is no nectary disc present.

The fruit comprises two pendulous follicles containing numerous seeds. The seeds are provided with a basal coma and are wind-dispersed.

2. Funtumia africana. The stamens are inserted at about the middle of the corolla tube and are completely included. The sides of adjacent anthers fit closely together forming a cone around the style-head. The anthers dehisce introrsely, shedding their pollen into a central chamber above the style-head (Fig. 26a). The anthers are differentiated as in Wrightia, with an upper region specialized for pollen production followed by a glabrous concavity, and below the concavity, a tuft of secretory hairs. However, in contrast to the long and exerted staminal filaments of Wrightia, those of Funtumia are very short. The result is that the tuft of hairs is actually located on the filament at about the level where they are adnate to the corolla tube (Fig. 25). These hairs (which also occur in the only other

species of the genus, F. elastica) are very conspicuous in microtome sections. They stain blue in the middle region, but at both ends they seem to be covered with a pinkish-staining sheath. It is possible that this is a thick cuticle or that the outer layer of the cell wall is lignified. However, these hairs are more specialized than the usual sort of lignified hairs that occur, for example, on the inner surface of the corolla tube or on the ovary in many Apocynaceae. They are very thick and appear to secrete a dark pink-staining substance that cements them to the style-head. It is also these sticky tufts of hairs that have taken over the function of trapping foreign pollen. This is reflected in the construction of the style-head. It has no pollen-capturing annulus at the base. It reaches its greatest diameter about in the middle, and tapers to cylindrical cones both above and below (Fig. 25). The lower cylinder is papillose, but does not appear to be secretory. The upper cylinder is specialized for adhesive production (Fig. 26b). Toward the middle the style-head becomes 5-angled. In this region the secretory hairs of the anthers are attached to the five angles of the style-head by thick, pink-staining mucilage. The style-head is radially interrupted at this level into five stigmatic zones which alternate with the places where the stamens are attached (Fig. 26c). Toward the base of the style-head the five strands of transmitting tissue unite (Fig. 26d) and continue as a single, solid cylinder through the style (Fig. 26e). The ovary is about one-third inferior and is surrounded at the base by a 5-lobed nectary. The carpels are congenitally fused only at the base of the ovary, and are apocarpous above. Each carpel contains ca. 150-300 ovules arranged in several rows. Placentation is axile (Fig. 26f).

The fruit is a pair of woody follicles which dehisce adaxially, releasing the many apically comose, wind-dispersed seeds.

3. Holarrhena floribunda. The floral structure is similar to that of Funtumia, with which it is closely related. The anthers form a cone above the style-head and dehisce introrsely, shedding their pollen into a central chamber (Fig. 28a). The anthers differ from those typically found in the Apocynoideae in that the anther body is not elaborated into long side wings (Figs. 28b, c). Therefore, sclerenchymatous tissue is also lacking. The hairs connecting the stamens to the style-head are at the base of the staminal filament and are similar to those described in Funtumia. The style-head is conical. The upper part is specialized for the production of adhesive. The stigmatic zone is around the periphery of the style-head at the level

where the diameter is the largest and the stamens are adnate to it (Fig. 28d). Below this the epidermis appears papillose, but not secretory. The pollen tube transmitting tissue encompasses the stigmatic region and extends as a column through the center of the style and along the placentae in the ovary (Fig. 27). The ovary is about one-third inferior and is apocarpous (Fig. 28e). Each carpel contains about 60 ovules in 8-9 rows.

The fruit is a pair of slender, coriaceous follicles which dehisce adaxially, releasing numerous dry, apically comose, wind-dispersed seeds.

4. Prestonia riedelii. From the level of stamen insertion upwards the corolla tube forms induplicate folds. In the five regions between the folds the corolla tube fits close against the dorsal sides of the anthers (Fig. 30a). The dorsal side of the anther is sclerenchymatous and elaborated into broad side wings that taper to elongate, slender basal appendages. The anthers form a cone around the style-head and dehisce introrsely before anthesis. The epidermal cells of the outer pollen sac walls are large with dark blue-staining walls. The outer pollen sacs open outwards until they are in a position very near those of the two neighboring anthers. The fit is very close, leaving only a narrow slit between adjacent anthers. At the same time, the inner pollen sacs open toward the center of the flower. During ontogeny the epidermis of the bases of the inner pollen sac walls develops large, conspicuous cells with dark-staining walls. When these cells come into contact with the upper style-head they become cemented to it by adhesive produced by the style-head and further extension of the pollen sacs is prohibited. In the median part of the anther the cells of the epidermis of the inner pollen sacs are tooth-like, and as the walls of the inner pollen sacs come into contact with the style-head these cells are pushed closer together. The teeth of the two epidermal layers of the two thecae interlock, with the dark blue-staining secretion filling the interspaces between them. The result of this postgenital fusion of the thecae is five separate pollen chambers that hold the contents of two thecae from adjacent anthers. The outer wall of the pollen chamber is formed by the adnation of adjacent outer pollen sac walls with each other; the inner wall is delimited by the adnation of the walls of the inner pollen sacs of adjacent anthers with the style-head (Fig. 30b). The ventral face of the anther is glabrous just below the thecae (Figs. 30c, d). Below this region is a tuft of very long, dark blue-staining secretory hairs that is adnate to the lower style-head (Fig. 30e). A region of cells that do not

stain with the dyes used is formed between the sclerenchymatous dorsal side and the tuft of hairs. The style-head is differentiated into functional regions that are synorganized with the stamens (Fig. 29). Functional differentiation is accompanied by morphological and histological differentiation. Thus changes in the nature of the secretory epidermis correspond to functional changes. The epidermis of the upper style-head contains considerable cytoplasm and stains pinkish-violet. It secretes a pink-staining exudate just to the level where the inner pollen sacs come into contact with it. This exudate agglutinates the inner pollen sacs to the style-head (Fig. 30b). Just below the bases of the thecae the style-head expands. The epidermis in this region stains bright blue and only a slight amount of dark blue-staining secretion was seen (Fig. 30c). Below this the style-head forms a cylinder that tapers at the base (Fig. 30d). The cells of the epidermis in this region contain a dense cytoplasm that stains pink-violet. These cells produce the main adhesive used for the transport of pollen. Below this the style-head is expanded where it is adnate to the anthers. The stigmatic region is located just below the level where the second expanded region of the style-head reaches its greatest diameter (Fig. 30e). At the level where the stamens are inserted on the corolla tube large protuberances form on the ventral (adaxial) side of the filaments. The protuberances are covered by glandular-appearing hairs. The protuberances surround the style. The glandular hairs of adjacent appendages interlock, dividing the corolla tube at this level into a central chamber and five separate peripheral channels. The channels between the protuberances are synorganized with the anthers as well as with the folds of the corolla tube, forming five channels that lead to the nectar. Two elongate, sclerenchymatous basal appendages, derived from adjacent anthers extend into the channel. They fit close together, with only a narrow slit between them (Fig. 30f). This slit guides the insect proboscis into the pollination structure as it is being withdrawn (Schick, 1982). The transmitting tissue extends from the base of the style-head as a cylinder through the style and along the placenta in the ovary. The ovary is surrounded at the base by a 5-lobed nectary. The two carpels are apocarpous and contain about 35 ovules each. Placentation is axile and the ovules are arranged in about 7-8 rows (Fig. 30g).

The fruit consists of two free follicles which dehisce along the ventral suture, releasing many, dry, apically comose, wind-dispersed seeds.

5. Parsonsia capsularis. The corolla tube is subrotate with reflexed lobes. The stamens are inserted in the lower third of the corolla tube, but due to their long filaments the anthers are totally exerted (Fig. 31). The structure of the reproductive organs is very similar to those of Prestonia. The anthers are differentiated, with the inner pollen sacs adnate to the upper style-head, forming five pollen chambers between adjacent anthers (Fig. 32a). Below this the anthers are concave. In this region the adhesive for pollen transfer is produced and accumulates in a ring between the style-head and the anthers (Fig. 32b). Below this the tuft of hairs is developed that is adnate to the style-head at its base where it is greatest in diameter. This is also the stigmatic region of the style-head (Fig. 32c). Below the stigmatic level the tufts of hair are no longer in contact with the style-head, but are connate at their sides, emphasizing the division of the corolla tube at this level into a central chamber and five peripheral channels (Fig. 32d). Just above the tops of the nectary lobes the staminal filaments fuse postgenitally, forming a ring around the style (Fig. 32e). The two carpels are completely postgenitally fused, producing an (ontogenetically) secondarily syncarpous, bilocular ovary with axile placentation. Each carpel contains about 25-35 ovules arranged in four rows (Fig. 32f). The ovary is about one-third inferior.

In fruit the mericarps remain fused, resulting in a capsule with valvular dehiscence. The seeds are dry, apically comose and wind-dispersed.

6. Mandevilla laxa. The reproductive organs are located in the lower part of the corolla tube. The stamens form a cone around the style-head and dehisce introrsely before anthesis. The anthers are differentiated; the dorsal side is modified into massive side wings and on the ventral side pollen production is restricted to the upper half, while the lower half is specialized for adnation to the style-head. The anthers are, however, different from those of all genera previously discussed. Except for the thecae and vascular bundles they are almost entirely composed of sclerenchymatic tissue. As the thecae open the outer pollen sacs of adjacent anthers meet; the inner pollen sacs are connate. In each anther the contents of one theca are shed into a chamber together with the contents of one theca of the adjacent anther, so that the pollen is contained within five peripheral chambers that are above the level of the style-head and do not come into contact with it (Fig. 34a). Unlike the genera with a gynostegium which have been described so far, in Mandevilla the ventral face of the anther below the thecae is not differentiated into a glabrous concave region and a tuft of hairs. Instead,

the ventral face of the anthers is uniformly covered by a short-celled, secretory epidermis. The content of the cells in this region is either more or less pale or stains pink. The cell walls do not stain and there is a thick cuticle. The cells secrete a pale pinkish substance that attaches practically the entire lower part of the anthers to the style-head (Fig. 33). This exudate spreads out from the sides of the ventral face of the anther where the cells are not in contact with the style-head and accumulates in five pockets between the anthers (Fig. 34b), where it apparently functions as the major adhesive in pollen transport. The style-head is shaped like a 5-lobed cone (Figs. 34b, c). It is uniformly covered by a short-celled epidermis, which has cells that are relatively rich in cytoplasm. The stigmatic region is at the base of the style-head under the lobes (Fig. 34d). The lobes project below the base of the style-head, forming a concavity (Fig. 34e) in which foreign pollen is trapped. The staminal filaments are bent inwards below the style-head and develop long hairs that surround the style (Fig. 34c). The pollen tube transmitting tissue continues as a cylinder through the style and along the placentae. The two carpels are apocarpous and surrounded at the base by a 5-lobed nectary. Each carpel contains about 200 ovules. Placentation is axile and the ovules are arranged in several series (Fig. 34g).

The fruit consists of two apocarpous follicles that dehisce along the ventral suture, releasing the many, dry, apically comose, wind-dispersed seeds.

4. Major Evolutionary Trends.

4.1. Gynoecium.

4.1.1. Primary and Secondary Syncarpy and Apocarpy.

It has been estimated that carpellary union has occurred 18-20 times during angiosperm evolution (Stebbins, 1974) and even a number of times within one family (Gut, 1966). The great majority of the genera of the higher dicot subclasses (i.e., excluding the Magnoliidae) have congenitally fused (syncarpous) gynoecia. In attempting to account for the overwhelming prevalence of syncarpy among the angiosperms, it is perhaps most instructive to regard this condition as a consequence of constraining selective pressure. One of the most important evolutionary achievements

of the syncarpous gynoecium is the presence of a compitum (Carr & Carr, 1961). This is a pollen tube transmitting tract that differentiates in the common central region of the fused carpels. This transmitting tissue forms a pathway interconnecting the carpels. Thus, even if only one stigmatic lobe receives pollen, once within the common transmitting region, the pollen tube may grow into any carpel. This not only allows an even distribution of pollen tubes among the carpels, but also enhances gametophytic selection (Endress, 1982), both of which carry an extremely high selective value.

The majority of the primitive dicots (Magnoliidae) are apocarpous, and therefore incapable of building a compitum of the sort described for syncarpous gynoecia. However, within this subclass a number of unusual alternative compitum types has evolved. In these species the common transmitting medium is usually mucilage, which is secreted by the upper part of the gynoecium and covers the carpel tips (Endress, 1979, 1980, 1982). Although generally not as efficient as a syncarpous compitum, these constructions nonetheless confer a competitive advantage to these primitive plants, and thus have a high selective value. This is demonstrated by the convergent evolution of such structures within the Magnoliidae.

Since apocarpy is generally regarded as a primitive condition in the angiosperms it is noteworthy that apocarpous representatives reappear in three separate higher dicot subclasses (Endress et al., in press). In these species it has been variously interpreted as being primary or secondary. Where apocarpy occurs in these groups it is almost always accompanied by a temporary postgenital fusion of at least the upper part of the carpels. In the region of postgenital fusion pollen tube transmitting tissue develops, forming a new type of compitum. Thus, in these species the apocarpous condition is best interpreted as phylogenetically secondary. In postanthetic flowers growth in the region of postgenital fusion does not keep pace with that of the expanding ovaries, causing the postgenital bond to rupture. Thus the carpels are again free at the time of dispersal. The fact that this condition has arisen independently in three higher dicot subclasses suggests that selection is favoring certain qualities of the apocarpous condition.

In most of the families in which apocarpy accompanied by a postgenital fusion of the carpel apices occurs it is rare, accounting for only a small percentage of the species, the others being syncarpous. In the Apocynaceae, however, this is not the case. Here the majority of the species are apocarpous. Furthermore, the greatest concentration of syncarpous genera is found

in the Carisseae, one of the most primitive tribes in the family. To understand why such a large-scale reversal should take place, it is first necessary to determine if it confers some selective advantage to the plant.

In the Apocynaceae I suggest that the major issue involved in the return to and maintenance of apocarpy is energetics. For example, the option of aborting one carpel when none of its ovules is fertilized, when it has been parasitised or otherwise damaged by insects, or when for other reasons the development of both carpels is not optimal, would allow a more efficient utilization of available energy (Endress et al., in press). Such innovations, which allow the plant to respond more plastically under stress conditions would carry a high selective value and would therefore tend to be perpetuated. A tendency toward the abortion of one carpel during development has been reported for genera of the Plumerioideae as well as the Cerberioideae (Rao, 1956; Léon & Alain, 1957; Fallen, in press), which lends support to this hypothesis.

The Carisseae and the Ambelanieae are the only characteristically syncarpous tribes in the Apocynaceae. In addition there is a tendency toward partial congenital syncarpy at the base of the ovary in the Rauvolfieae and the Cerberioideae, and partially syncarpous species appear sporadically in other tribes of the Plumerioideae and in the Tabernaemontanoideae. Only three examples of completely syncarpous gynoecia have been reported for the Apocynoideae: Parsonsia (Schumann, 1895), some species of Wrightia (Ngan, 1965), and one species of Alafia, A. multiflora (A. Leeuwenberg, pers. comm.). In the case of Parsonsia the gynoecium is apocarpous at initiation and fuses completely during ontogenetic development. I suspect the same will prove to be the case for species of Wrightia and Alafia multiflora, but to date I have not been able to obtain buds which were young enough for an ontogenetic study.

The syncarpous gynoecia which occur in the Apocynaceae are thus of two very different sorts:

1. congenital (primary) syncarpy, which is characteristic for the Carisseae and the Ambelanieae.
2. postgenital (secondary) syncarpy in some Apocynoideae (and Allamanda).

4.1.2. Style-head.

In the gynoecium of the Apocynaceae the postgenital fusion process is initiated quite early in floral ontogeny. The carpel apices fuse together along their flanks and the original epidermis in the region of fusion can

no longer be detected (Boke, 1949; Walker, 1975). The postgenitally fused region is the fusion product of the upper parts of 2(-5) carpels and represents a new level of morphological complexity with corresponding new adaptive potential. Morphogenesis of this organ proceeds at a rapid rate, so that it is at a very advanced stage while the bud is still very small. The early and rapid development is an indication of the complexity as well as the importance of this organ in later developmental stages. This new organ is variously known as the style-head, stigma-head, or clavuncle. I have adopted the first term, as I find it the least ambiguous.

In its primary capacity the style-head functions as a compitum (Walker, 1978) and allows increased competition among pollen tubes. In addition, selection acting on the style-head has resulted in the emergence of novel functions being carried out by this organ, and has produced an elaborate pollination mechanism, which reaches its highest degree of complexity in the Asclepiadaceae.

Evolution of the style-head is characterized by a number of coadaptive functional shifts. This has taken place mainly through progressive specialization of the organ parts of the style-head, resulting in a complex pattern of morphological/functional regions. The major trend in the specialization of the style-head is the tendency toward its vertical compartmentalization into three functional regions concerned with pollen storage, adhesive production, and stigma, respectively. This has been augmented by a secondary trend for the style-head to be radially interrupted into five segments due to the intervention of the androecium (Schick, 1980, 1982). Although the removal and reception of pollen occurs at five independent sites, these are interconnected by the compitum, allowing a uniform distribution of the pollen tubes to the ovules.

In his first paper on the style-head of the Apocynaceae Schick (1980) recognized only two style-head types: the simple, club-shaped "Plumeria-type", and the more highly differentiated "Allamanda-Nerium type". The first of these is, in my opinion, a heterogeneous assemblage containing primitive genera with relatively unspecialized style-heads, together with highly advanced genera with style-heads which appear simple due to a secondary loss of parts. The second group is likewise composed of heterogeneous elements, and does not reflect true relationships among genera.

In the second article Schick (1982) considered the style-head and anthers as a functional unit and recognized five organizational levels within the family. He correctly removed the advanced members from the "Plumeria-type";

these formed the new "Apocynoideae-type". The "Plumeria-type" represents the most simple organizational level, the members of which lack precise co-adaptations between the gynoecium and androecium. The "Apocynoideae-type" is the most advanced and is characterized by the postgenital union of the gynoecium and androecium. Between these two extremes are three intermediate levels: the "Catharanthus-, Vinca-Thevetia-, and Allamanda-type". These categories are much more natural than those of his previous paper (Schick, 1980), and to a large extent reflect true phylogenetic relationships within the family.

I recognize four levels of complexity in the style-head of the Apocynaceae, two of which coincide with the style-head type in the organizational levels proposed by Schick (1982). The Level 1 style-head occurs in what are usually regarded as the most primitive genera. The style-head is morphologically undifferentiated and is covered by a uniform layer of secretory epidermis. It is supposed that there is a corresponding lack of functional division as well. Although undifferentiated in this sense, the style-head in these genera is already considerably specialized, carrying out the dual function of stigma as well as the production of adhesive for pollen transport. The organizational level where an organ functions in two capacities is a common transitional stage in a transfer of function (Stebbins, 1974; Mayr, 1979). In Alyxia ruscifolia, a genus with a style-head of this type, the entire style-head is receptive to pollen tube penetration according to Schick (1980). This type of style-head is found only in the Plumerioideae, and corresponds to the type of style-head in Schick's (1982) "Plumeria-type".

In the Level 2 style-head the following basic regions of the style-head may be recognized from top to bottom:

1. An upper ring of longer hairs onto which the anthers shed their pollen. This spreading ring helps to partition the pollen storage region from the adhesive-producing region.
2. The main body of the style-head, which is cylindrical and has a secretory epidermis composed of short, columnar cells directed more or less perpendicular to the longitudinal axis of the style-head. These specialized cells are responsible for the secretion of the adhesive used in pollen transport.
3. A lower wreath of longer hairs, or a ring of downward directed, elongated cells which are fused together into an annular "collar" that projects below the base of the style-head body. These structures act as scrapers to accumulate foreign pollen from insect visitors (Hildebrand,

1867; Demeter, 1922; Schick, 1982).

4. A stigmatic region that is located just below the pollen-trapping structure, often in the hollow under the base of the style-head (Demeter, 1922; Schick, 1982).

Since I present the evolutionary levels of the style-head and the anthers separately, whereas Schick (1982) presents organizational levels of the gynoeceum and the androeceum as a unit, his "Catharanthus-, Vinca-Thevetia-, and Allamanda-type" are all encompassed by my Level 2 style-head.

The Level 3 style-head occurs only in the Apocynoideae and is associated with the attainment of a gynostegium. The style-head shows basically the same differentiation as a Level 2 style-head, except that the anthers are adnate to it. This type of style-head represents an important transitional stage in a transfer of function involving the pollen-trapping apparatus. Although the annulus or wreath of longer hairs is still present at the base of the style-head, the function of pollen trapping has been taken over to a large extent by the hairs on the ventral face of the adnate anthers. The Level 3 style-head coincides for the most part with Schick's (1982) "Apocynoideae-type" organizational level.

In some advanced Apocynoideae the pollen trapping function has been completely transferred to the anthers. The pollen trapping structures at the base of the style-head have been secondarily lost. This is generally accompanied by a loss of the upper ring of hairs as well. This represents the Level 4 style-head. Since Schick (1982) did not take into account this transfer of function, he did not distinguish this category from the "Apocynoideae-type" organizational level.

It is noteworthy that the extreme tips of the carpels do not fuse during style-head formation. In the mature flower they are usually noticeable as two apical appendages atop the body of the style-head. In some genera (e.g., Anechites, Cameraria, Plumeria) they are quite large and conspicuous.

The tissue in the upper region of the style-head usually contains many tracheid groups and the free apices may be composed almost entirely of tracheid groups. I suggest that this parallels the adaptive shift from stigma to adhesive production which has taken place in the upper region of the style-head. The tracheid groups would play an integral role in the imbibition and storage of moisture. It is important that the style-head remain moist to prevent the adhesive from drying out. This is crucial for the precision functioning of the pollination mechanism.

4.1.3. The Location of the Stigma.

A recurring question in studies of the floral biology of the Apocynaceae is the location of the stigma. The difficulty is due to the complex nature of the style-head. The vertical walls of the style-head have been described as the receptive zone due to the secretory epidermis (Sprengel, 1793; Church, 1908; Hickey & King, 1981). Other authors refer to the free apices of the style-head as the stigmata (Allorge, 1976; Beentje, 1978; De Jong, 1979; Boiteau, 1981; Zwetsloot, 1981). In fact this belief prompted Miers (1878) to coin the term "clavuncle" to distinguish this "fleshy cylindrical process" (the style-head) from the "two stigmata" upon its summit. In all of the genera that I have investigated these apical appendages appear to be non-receptive, often being composed principally of tracheid groups.

In most taxonomic studies the entire style-head is referred to as the stigma or stigmatic head, with no attempt made to determine the location of the actual receptive region (Stapf, 1902; Woodson, 1933, 1951; Ezcurra, 1981; Kupicha, 1981). Attempts have been made to identify the stigmatic region via pollen tube growth, but subtleties between germination and penetration present complications (Demeter, 1922; Schick, 1980).

I have basically used histological differentiation to determine the location of the stigmatic and transmitting tissue in the style-head. In addition, there are two "rules of thumb" which I have found to be very useful. First, the stigmatic region is usually located at the level where the style-head is largest in diameter. This is typically at the base, but must not be (see Fig. 25). Second, the stigmatic tissue is located at the level of the pollen grain trap or just below it. According to the complexity of the style-head and functional shifts in "pollen trapping" the location of the stigmatic region for the various style-head levels is as follows:

Level 1.--No specialized structures developed for the capture of pollen grains from insect mouthparts. Pollen grains simply stick to the adhesive of the style-head. The entire style-head (except the uppermost "tracheid-containing" region) is receptive.

Level 2.--As the insect proboscis passes by the basal "collar" of the style-head pollen grains are scraped off and accumulate beneath in the stigmatic hollow.

Levels 3 and 4.--Pollen is removed from the insect proboscis by brush-like groups of hairs on the ventral face of the anthers, which, in conjunction with the adhesive secreted by the style-head, agglutinate the anthers to the style-head. The stigmatic region is at the level of the

the attachment of the anthers or slightly below.

4.2. Androecium.

The evolution of the androecium in the apocynaceous flower follows a pattern similar to that for the gynoecium (with which it is closely co-adapted), with major evolutionary trends being characterized by functional shifts associated with morphological and histological specialization of the anthers. In the Level 1 condition the anthers are unspecialized. The thecae are simple and rounded at the base and dehiscence is collateral; the dorsal part of the anther is unmodified. This is the typical condition for the Plumerioideae. From this primitive state two different evolutionary trends are evident.

One, which has achieved only moderate success, has basically involved modifications of the connective. It becomes enlarged at the base, causing the thecae to become sublateral, while the apex tends to develop an acumen, which can become very exaggerated (e.g., Skytanthus). This Level 2 anther is characteristic for the Cerberoideae.

The other, more successful trend is characterized by functional shifts associated with morphological and histological differentiation of other parts of the anther. Within this evolutionary trend two levels of complexity can be distinguished. In the first, representing Level 3 anthers, the tissue in the dorsal part of the anther is sclerenchymatic and elaborated into massive side wings with caudate basal appendages that extend below the thecae. This level of complexity is characteristic for the Tabernaemontanoideae, as well as the closely related Ambelanieae of the Plumerioideae.

Level 4 represents the final, and most successful evolutionary phase of the anthers. The anthers are differentiated as in Level 3, but in addition, tufts of hair develop on the ventral face of the anther below the level of the thecae. These hairs are special adaptations for affixing the anther to the style-head. They become intimately enmeshed in the papillae of the style-head, and the adhesive produced by the style-head fills the spaces between the interlocking trichomes, cementing the bond. This bond is so strong in most members of the Apocynoideae that attempts to pull an anther free from the style-head usually result in a chunk of the style-head tearing away with it. This condition is diagnostic for the large subfamily Apocynoideae and is assumed to be the most important step in its explosive radiation. It is interesting that a similar sort of bond has evolved in Thevetia (Gensel,

1969), which is presumed to be the most advanced member of the Cerberoideae.

In a few instances (e.g., Funtumia and Mandevilla) it was found that the tufts of hair on the ventral face of the anther are secretory and also produce adhesive. In Funtumia it appears that both the style-head and the anther hairs produce adhesive, but in Mandevilla this function seems mainly to have been taken over by the anthers. This is an interesting transfer of function that, to my knowledge, has not previously been reported in the family.

A primary function of the tufts of hairs, and one that seems to have gone unnoticed, is the increasing role they play in the removal of pollen from insect visitors. They form brush-like structures which scrape the pollen grains from the insect proboscis as it is withdrawn. The pollen is trapped in and below the brushes against the style-head.

A feature of the stamens which is a valuable taxonomic tool and has been largely overlooked is the comparative histology. Sclerenchyma is present only rarely in the stamens of flowering plants (Schmid, 1976). It is restricted to certain groups where it has arisen independently in response to very different selective pressures. In the Apocynaceae the occurrence of sclerenchyma is a functional coadaptation toward the perfection of the gynostegium. The primitive Plumerioid anther lacks sclerenchyma; support is provided only by endothecial-type thickenings. In the more advanced Tabernaemontanoideae and Ambelanieae the anthers develop sclerenchymatous side wings, and in many genera of the Apocynoideae most of the anther may be composed of sclerenchymatous tissue (see Figs. 29-33). The presence of sclerenchyma in the anthers of the Apocynaceae is therefore considered to be a derived condition.

Another histological differentiation of the anthers that seems to be correlated with the occurrence of sclerenchyma is a zone of special tissue with cell walls that do not stain (with safranin and astra blue). This tissue often forms on the dorsal side of the anther, where it is joined to the corolla tube. This feature has also been reported by Allorge et al. (1980). They state that this "tissu moteur" is a diagnostic character of the Tabernaemontanoideae that may be used to distinguish this subfamily from the Apocynoideae. However, I have found this type of tissue often in members of the Apocynoideae, and in the Ambelanieae as well--thus, in the three main groups in which the anthers contain sclerenchymatous tissue. It seems, then, that the presence of this tissue is better interpreted functionally than phylogenetically. Like Allorge et al. (1980) I suppose that it allows the otherwise rigid cone of anthers a certain amount of flexibility, which is necessary for the proper functioning of the pollination mechanism. This would be espec-

ially important in cases where the massive, rigid anthers are subsessile.

A phenomenon that I have observed in many species of Apocynaceae with sclerenchymatic tissue in the anthers is the occurrence of air spaces around the vascular bundle of the anther. Although this condition is more pronounced in anthetic flowers than in buds, it is already observable in very young buds, and therefore does not seem to be simply due to expansion during development. Whether it is incidental or serves a specific purpose is not known.

In earlier studies on the Apocynaceae, in which the structure of the anthers was considered, attention centered on the morphological differentiation of the side wings. Their histological differentiation was not discussed, nor was the functional significance of the hair tufts on the ventral face of the anther. It was generally believed that the side wings were the result of the suppression of pollen-producing tissue of the outer locules and of the subsequent transformation of the sterile part of the outer locules into the elongate basal appendages which form part of the sophisticated pollinating apparatus (Schumann, 1895; Demeter, 1922). More recent studies suggest that the modified basal appendages have not been formed by the "transformation" of the outer locules (Baum, 1953; Safwat, 1962), but have evolved independently by enlargement, and by a radiation of adaptive types into a new functional niche (compare with Kunze, 1982).

This also seems to be the best explanation for the evolution of the special tufts of hairs which occur on the ventral face of the anther and/or staminal filament. This feature has undergone considerable radiation and exhibits a wide variety of structural types. This structure was termed the "retinacle" by Pichon (1950) and formed the basis of his tribal classification of the Echitoideae (= Apocynoideae) (Pichon, 1948d).

4.3. Gynostegium.

Although the term gynostegium has usually been used only in the Asclepiadaceae, the relationship of the gynoecium and the androecium in the more advanced Apocynaceae (Apocynoideae) is only a slightly modified version of that found in the Asclepiadaceae (compare with Kunze, 1982). In the Apocynoideae the postgenital fusion of the two organs begins later in the ontogeny and is thus less complete than in the Asclepiadaceae. The basic design and function of this feature, however, is the same, and therefore, it should be referred to as a gynostegium in both families.

5. Floral Biology.

The floral biology and pollination mechanism of various members of the Apocynaceae have received considerable attention from early botanists (Sprengel, 1793; Delpino, 1867; Hildebrand, 1867; Ludwig, 1880; Frye & Blodgett, 1905; Demeter, 1922). These studies were mostly made on temperate species. (Apocynum was especially popular due to its reputation for trapping flies (Ludwig, 1880; French, 1883)). Recently two excellent papers by Schick (1980, 1982) have contributed considerably to the subject.

The basic floral structure of the Apocynaceae is relatively fixed. With a few exceptions the flowers are radially symmetrical, tubular, pentamerous except for the bicarpellate ovary, and are pollinated by insects. (The only genera which are known to show secondary adaptations for bird pollination (see Stiles, 1981) belong to the New World Apocynoideae, and are presumably pollinated by hummingbirds). The anthers are introrse (latrorse in the Cerberoideae) and shed their pollen shortly before anthesis. In the majority of the genera the floral reward is nectar. In a few genera no nectar-secreting tissue has been found. But it has not been demonstrated whether they are true deceptive flowers, offering no reward, or if an alternative floral reward is provided.

The pollination mechanism in the Apocynaceae relies on the proboscis of an insect to transfer pollen. The proboscis is extended into the floral tube as the insect probes for nectar. As it is withdrawn, it moves toward the center, passing first the lower ring of hairs, below which, in the (generally) stigmatic zone the foreign pollen tends to accumulate. It then slides past the middle secretory cylinder where it becomes coated with adhesive produced by the style-head. As the proboscis moves up through the upper chamber it comes into contact with pollen grains which have been shed from the anthers. The pollen grains become stuck to the adhesive, coating the proboscis (Rowley, 1980; Schick, 1980, 1982).

In many genera the throat of the corolla tube is constricted, assuring that the proboscis is guided toward the center of the flower as it is withdrawn. In other cases (such as Vinca, Thevetia, Cerbera, etc.) protuberances of the corolla tube above and/or below the staminal filaments guide the proboscis along the correct path. The staminal filaments may also become buckled toward the center of the flower, forming "knees" upon which the lower surface of the style-head rests. In Thevetia (including Cascabela (Lippold, 1980)) and in Vinca the bend of the staminal filaments fit precisely into grooves in the lower part of the style-head, which tends to partition the

corolla tube into five chambers at this level.

In the Tabernaemontanoideae the style-head is usually 5-lobed in the upper part and is surrounded by the anthers. The effect is that of five channels that alternate with the lobes of the style-head. Often intrastaminal appendages of the corolla tube are present that emphasize the channelizing effect.

In the Apocynoideae the role of guiding the insect's proboscis is shifted more and more to the androecium. The anthers develop elongated sclerenchymatous side wings which extend below the thecae, and the special hairs on the ventral wall, by which they are attached to the style-head. Thus the style-head is held firmly in position by the surrounding anthers. The apices of the anthers close over the style-head and the sclerenchymatic sides of adjacent anthers fit closely together, being separated by only a narrow slit. It is through these slits that the insect proboscis is threaded into the stigmatic, adhesive, and pollen chambers (Schick, 1982). The similarity of structure of the floral mechanism in the Asclepiadaceae (Corry, 1883; Demeter, 1922; Kunze, 1982) is unmistakable (Safwat, 1962; Schick, 1982).

In addition to insuring that the insect proboscis is guided precisely through the pollination organs, the close fit of the anther cone insulates the style-head from the outside environment and protects the adhesive from desiccation. With this protective roles having been gradually taken over by the androecium, the restraints on the corolla tube diminished. The constrictions of the throat and other elaborations tending to close the mouth of the corolla tube, such as suprastaminal appendages and hairs were no longer so important once the style-head became encased within the sclerenchymatic anthers. Therefore, it is first in genera of the Apocynoideae that unobstructed corolla tubes are encountered. A progressive shortening of the corolla tube has lead to campanulate or subrotate flowers with the style-head and its surrounding cone of anthers exerted in advanced genera such as Apocynum and Forsteronia.

6. Evolution and Systematics.

6.1. Selected Topics.

6.1.1. Pleiocarpeae.

In his treatment for Engler & Prantl's *Pflanzenfamilien* Schumann (1895) included all of the apocynaceous genera with more than two carpels known to him at the time in his tribe Pleiocarpeae. Tribal delimitation based on a single character is too simplistic; the situation in nature is usually considerably more complicated. Thus, it is not surprising that the resulting assemblage was unnatural. It included: *Notonerium*, which is a Boraginaceae, *Lepinia* and *Lepiniopsis*, which belong to the tribe Rauvolfieae, and *Pleiocarpa*. Pichon (1948a) described Schumann's Pleiocarpeae as a heterogeneous and unnatural group, and dismantled the tribe. He included *Pleiocarpa*, *Picralima*, *Hunteria*, *Polyadoa*, *Tetradoa*, *Pleuranthemum*, *Comularia* and *Carpodinus* in his subtribe Pleiocarpineae. Pichon's tribal classification is based almost entirely on whether the fruit is dry or fleshy and dehiscent or indehiscent (Pichon, 1948a, c). Thus, because of their fleshy, indehiscent fruits, he placed the subtribe Pleiocarpineae in the tribe Carisseae. In using basically a single character to determine tribal limits, Pichon was forced by his own criteria to include the Pleiocarpineae in the tribe Carisseae, despite dissimilarities that set them apart from the other subtribes (Pichon, 1952, 1953b). Nevertheless, this position has generally been accepted (Allorge et al., 1980; Leeuwenberg, 1980).

I agree with Pichon (1948a) that the fruit (and seeds) provide some of the most valuable taxonomic characters available to establish a natural classification within the family. However, by assigning so much weight to one character at the expense of others, subtleties are lost and important relationships may be overlooked. Certainly the Pleiocarpineae is a homogeneous, natural group and shows alliance to the Carisseae by their fleshy, indehiscent fruits with flattened seeds. But the fact that they are apocarpous sets them apart from the rest of the Carisseae, where the carpels are congenitally fused. Of more systematic significance is the number of characters that they share with *Aspidosperma* and the genera around it.

The Pleiocarpineae have gaps in the corolla tube that occur behind the staminal filaments where the congenitally fused lower corolla tube meets the postgenitally fused upper part. The postgenital fusion of the petal margins of the upper corolla tube proceeds basipetal so that the last place to fuse

is directly behind the insertion of the staminal filaments. (For other genera see: Boke, 1948; Walker, 1975, 1978; Nishino, 1982). The fusion process begins relatively late in floral ontogeny and, at anthesis in many genera, epidermal cells may still be distinguished in this region, or, as in the case of the Pleiocarpineae, gaps.

The corolline gaps were first mentioned by Woodson (1951) for the neotropical genus Aspidosperma. He reported that these gaps did not occur in Geissospermum or Diplorhynchus, genera which in many other respects show a close relationship to Aspidosperma, and therefore that the gaps were a diagnostic feature of the genus Aspidosperma. Markgraf found similar gaps in the Madagascan endemic Stephanostegia and suggested a close relationship between the two genera (Markgraf, 1974).

I have also found such gaps in anthetic flowers of Geissospermum, Haplophyton, and Vinca. It seems, then, that this condition may be relatively common in the tribe Plumerieae. It is therefore interesting to find that they also occur in the Pleiocarpineae. Pichon (1953b) reported slits behind the stamens in the corolla of Pleiocarpa. My study confirms this. I have also found them in Picralima. I expect them to be present in Hunteria as well, but to date I have been unable to obtain fixed material of this genus for study. Allorge (1975) reported gaps in the corolla tube of Allamanda, but my sections have failed to reveal this. It is possible that the flower that she sectioned was immature, or that the character is not constant within the genus. (Her report concerned A. grandiflora, while my sections are of A. schottii).

The Pleiocarpineae also resemble Aspidosperma and Geissospermum in the morphology of the style-head. It is roughly cone-shaped and shows very little morphological or anatomical specialization.

The pollen of both the Pleiocarpineae and of Aspidosperma and Geissospermum is poly-zonocolpate (terminology after Radford et al., 1974). This type of pollen was described and illustrated by Marques & Melhem (1966) for Aspidosperma tomentosum, which, in their terminology, is described as being "4-pseudocolpato-4-colpate". I have not observed this type of pollen in any other members of the Carisseae.

Chemical evidence provides further support for a close relationship between the Pleiocarpineae and the complex of genera in the Plumerieae centered around Aspidosperma. In the Apocynaceae indole alkaloids with a C₉- or C₁₀-monoterpene moiety have reached a high degree of complexity and are useful in determining systematic relationships between genera. In addit-

ion, because their biosynthesis proceeds in a number of successive steps, the evolution of these alkaloids can be reconstructed and may thus be used as indicators of the evolutionary pathways of the taxa involved (Boiteau, 1975; Kisakürek, et al., 1983).

The occurrence of specific complex plumerane-type alkaloids in the Pleiocarpineae as well as in Aspidosperma, Geissospermum and Haplophyton provide strong support for their close phylogenetic relationship (Ganzinger & Hesse, 1976; Kisakürek et al., 1983). Furthermore, the chemistry of the other members of the Carisseae is quite different (M. Hesse, pers. comm.). This suggests that the Pleiocarpineae represent an important evolutionary link between the Carisseae and the Plumerieae.

Geissospermum, with its fleshy fruits and dextrorsely contorted corolla lobes has always been taxonomically problematic. It has generally been placed in the Tabernaemontaneae (Müller-Argoviensis, 1860; Miers, 1878; Baillon, 1891; Schumann, 1895) simply because of its fleshy fruits, which superficially resemble those of Tabernaemontana. Markgraf (1938) was the first to recognize that, although the fruits of Geissospermum are fleshy, they are essentially different in structure from those of the Tabernaemontaneae, and placed Geissospermum next to Aspidosperma, though all other members of the subtribe Aspidospermatinae have dry follicles and winged, wind-dispersed seeds. So, although this new taxonomic position did reflect a natural relationship, it was not completely satisfactory (Markgraf, 1939; Pichon, 1948c).

By assigning Geissospermum a position in the Pleiocarpineae, both its close relationship to Aspidosperma as well as its fleshy fruits and seeds without arils no longer pose a problem.

The Pleiocarpineae also show a more distant affinity to Kopsia and Ochrosia. It is possible that Kopsia and Ochrosia stem from Pleiocarpineae ancestors in which the fruits evolved adaptations for sea water dispersal and which underwent a subsequent radiation in island habitats, with Ochrosia having attained the more derived condition. There is some chemical evidence to lend support to this hypothesis (Ganzinger & Hesse, 1976). But I am unable at present to determine the exact nature of the interrelationships between the Pleiocarpineae, Rauvolfieae, and Cerberoideae.

In view of these findings, I believe that phylogenetic relationships within the Plumerioideae are better reflected by promoting the Pleiocarpineae to tribal rank. I agree with Leeuwenberg (1980) that Polyadoa, Tetradoa, Pleuranthemum, Comularia and Carpodinus are too narrowly circumscribed and

should be reduced to Hunteria. I propose that the tribe Pleiocarpeae include the following genera: Picralima, Hunteria, Pleiocarpa, and Geissospermum.

6.1.2. Allamanda.

At anthesis the ovary of Allamanda is unilocular with parietal placentation (Fig. 17, 18h). Therefore, it has frequently been included in the tribe Carisseae (DeCandolle, 1844; Bentham & Hooker, 1876; Schumann, 1895). This is unfortunate, as Allamanda shows not even a remote affinity to this tribe. The fruit of Allamanda is a dry, spiny, valvate capsule, and has seeds with an undulate margin--completely different from the fleshy, indehiscent fruits of the other members of the Carisseae. For this reason many authors have preferred to assign it to its own tribe in the Plumerioideae (Müller-Argoviensis, 1860; Miers, 1878; Baillon, 1891; Pichon, 1948c; Wagenitz, 1964). Allorge (1975) claims that the anthers are attached to the style-head and places it in the Apocynoideae.

Andersson (1931) describes the ovary as syncarpous and unilocular except at the very base, where two locules can be discerned. He notes that the boundary between the two carpels is marked by a shallow groove that runs down the outside of the ovary.

Woodson (1930) and Allorge (1976) discuss fusion of carpels in the Apocynaceae, and point out that in Allamanda the parietal placentae are sterile in the central region and that epidermal cells can still be distinguished at the juncture of the two carpels. Both interpret the condition phylogenetically, and cite these "relictual" characters in the genus Allamanda, specifically, as evidence that evolution in the Apocynaceae has proceeded from an apocarpous, bilocular ovary through a syncarpous, bilocular intermediate form to a derived syncarpous, unilocular condition. If this hypothesis is correct one should find epidermal cells in the region where the two carpels are joined in those genera of the Carisseae which have syncarpous, bilocular ovaries. But in these genera the tissue is continuous and uniform.

A study of the ontogenetic development of the gynoecium in Allamanda reveals that, unlike the genera of the Carisseae, where the ovary is congenitally syncarpous, in Allamanda the syncarpous, unilocular condition is derived. The ovary is initiated as two separate carpels that fuse post-genitally during development. Fusion between the two carpels takes place before closure of each individual carpel, resulting in parietal placentation.

Although this type of development has not been previously reported in the Apocynaceae, it is common in the Gentianaceae (e.g., Frasera (McCoy, 1940), Centaurium (Baum, 1949; Vijayaraghavan & Padmanabhan, 1969), Gentiana (Leinfellner, 1951), Encicostemma (Padmanabhan et al., 1978) and Pleurogyne (P. Endress, pers. comm.). This type of development is illustrated in the following figure series.

At initiation the floral apex develops into a raised area with an indentation between the two carpel primordia (Fig. 37). At a slightly later stage the carpel primordia begin to develop a concavity on their ventral wall (Fig. 38). As the carpels enlarge the ventral concavities become more pronounced. The ovary is apocarpous above and begins to fuse postgenitally at the base (Fig. 43). At this stage the lobes of the nectary disc begin to take shape (Fig. 39). The ovules are initiated as two protuberances at the edge of the ventral slit in the postgenitally fused region (Fig. 44). As growth continues the postgenital fusion process continues from the base upwards. The nectary disc is distinct from the ovary, and the style-head begins to differentiate (Fig. 40). At this stage a rift begins to form in the median plane of the ovary, splitting the tissue along the ventral slit of the two carpels. As development proceeds the gynoecium is differentiated into the style-head, style, and ovary regions (Fig. 41a). The suture along the region of postgenital fusion is still evident from the outside (Fig. 41b) and the unfused apices of the style-head begin to differentiate (Fig. 41c). The succeeding stages are for the most part concerned with elongation and enlargement; differentiation of the style-head continues. The basal annulus is formed and the cells of the epidermis become papillose in preparation for the onset of the secretory phase. Inside, periclinal cell divisions take place shortly after fusion so that the juncture of the two halves is no longer distinguishable (Fig. 45a). A suture is still visible in the postgenitally fused ovary region (Fig. 42), and within the ovary the epidermis between the two carpels is still detectable (Fig. 45b).

Allamanda has an unusual complement of characters that makes it difficult to determine its relationship to other genera of the Apocynaceae. The globose, echinate fruits which have valvate dehiscence are unlike the fruit of any other genus in the family. The seeds are usually described as being "winged", which could indicate a connection with the Plumerieae. However, the seeds do not have the thin, papery wings which are typical for the Plumerieae. Instead, the margin of the flat seed is undulate and irregularly thickened and it appears to be inefficiently constructed for wind dispersal.

About half of the species of Allamanda have calycine squamellae (which do not occur in the Plumerieae) and infrastaminal protuberances of the corolla tube. Both of these features occur commonly in the Tabernaemontanoideae and also in certain genera of the Cerberoideae. But it is difficult to conceive of how the dry, capsular fruit and marginate seeds could have evolved from a Tabernaemontanoid ancestor.

Allamanda shares the following features with the Cerberoideae: sessile to subsessile anthers, protuberances of the corolla tube, marginate or winged seeds, and a brown colored embryo. However, this is not sufficient to indicate a phylogenetic relationship between the two groups. Furthermore, the fact that the pattern of gynoeceum development is unique within the family suggests that Allamanda occupies an isolated position within the Apocynaceae (see Fig. 47) and supports assigning it tribal status within the Plumerioideae.

6.1.3. Holarrhena.

The genus Holarrhena has a confusing taxonomic history. It has been placed in the Plumerioideae by some authors (Bentham & Hooker, 1876; Schumann, 1895; Pichon, 1950; Allorge et al., 1980; De Kruif, 1981) and in the Apocynoideae by others (DeCandolle, 1844; Miers, 1878; Stapf, 1902). The dextorsely contorted corolla lobes and apically comose, wind-dispersed seeds indicate that it belongs in the subfamily Apocynoideae. Furthermore, Holarrhena lacks indole alkaloids, which are characteristic for the Plumerioideae, but contains steroidal alkaloids, which have otherwise been isolated only from members of the subfamily Apocynoideae (Ganzinger & Hesse, 1976; Bisset, 1981; Kisakürek et al., 1983). Twice already it has been recently recommended that the genus be moved to the Apocynoideae based on its alkaloid chemistry (Ganzinger & Hesse, 1976; Kisakürek et al., 1983). Despite this evidence, all of the more recent authors have placed Holarrhena in the tribe Plumerieae of the subfamily Plumerioideae (Pichon, 1950; Allorge et al., 1980; De Kruif, 1981).

The problem stems from the seemingly simple structure of the anthers. They are not agglutinated to the style-head and they lack the conspicuous, elongated side wings that are typical for members of the Apocynoideae. Because the adnation of the anthers to the style-head is the single most definitive character commonly used in taxonomic keys to separate the Plumerioideae from the Apocynoideae, this character was given more weight than the

combined body of evidence indicating the rightful position of Holarrhena within the Apocynoideae.

Of the four recognized species of Holarrhena (De Kruif, 1981), I have studied three (H. floribunda (G. Don) R. Br.; H. mitis (Vahl) R. Br.; H. pubescens (Buch.-Ham.) Wall. ex G. Don) anatomically and histologically in serial sections. In each case the stamens are agglutinated to the style-head by glandular hairs which are found, not on the ventral face of the anther, but at the base of the staminal filament (Fig. 46). Furthermore, the hairs are of an advanced type that I have never observed on stamens of genera in the Plumerioideae. I have found similar hairs only in the genus Funtumia.

In addition, as Stapf (1902) pointed out for the two African species (H. pubescens and H. floribunda), the anthers of Holarrhena actually do have side wings, albeit very much reduced, which are adnate to the connective. The side wings are more pronounced in H. mitis, an endemic species from Sri Lanka. The presence of the side wings is easily confirmed by a careful comparison of the anthers of Holarrhena with those of typical members of the Plumerioideae.

I suspect that Pichon's (1950) subtribe Holarrheninae, composed of Holarrhena, Carruthersia and Spirolobium will prove to be an unnatural group. His hypothesis that the poorly developed anthers of the Holarrheninae are an indication of the primitiveness of the group and that this subtribe might represent the ancestral stock which gave rise to the Apocynoideae is not very convincing. On the contrary, it seems more probably that the structure of the anthers is a derived condition, especially considering the highly specialized secretory hairs that affix the stamens to the style-head. A comparative study of the three genera would be interesting and might shed some new light on the intrafamilial classification.

Demonstrating the adnation of the stamens to the style-head in Holarrhena removes the last objection to its association with the Apocynoideae. Thus, based on the following characters, I suggest that Holarrhena be placed in the Apocynoideae:

1. Dextrorse aestivation of the corolla lobes.
2. Union of the stamens with the style-head.
3. Apically comose seeds.
4. Morphologically differentiated anthers.
5. Presence of steroidal alkaloids and absence of indole alkaloids.

6.2. A Survey of the Major Taxonomic Groups.

The following is a brief survey of the general characteristics of the groups represented in the phylogenetic diagram in Fig. 47. Four subfamilies are recognized. In addition to the two large subfamilies, Plumerioideae and Apocynoideae, the Cerberoideae and the Tabernaemontanoideae are considered distinctive enough to warrant subfamilial status. The Apocynoideae established by Woodson (1930) is not considered worthy of the rank of subfamily and is here considered as an element of Schumann's (1895) Echitoideae, the name of which must be changed to Apocynoideae, since Apocynum, the type genus of the family, occurs in this subfamily.

The P l u m e r i o i d e a e is the most primitive and the most heterogenous subfamily. It is characterized by the presence of indole alkaloids with a broad range of complexity. Aestivation of the corolla lobes is usually sinistrorse. The anthers are usually unspecialized and are free from the style-head. In all genera the style-head produces adhesive used for pollen transport, and style-heads of both the first and second level of complexity occur (see Sect. 4.1.6.). Six tribes are recognized within the Plumerioideae. (Following Boiteau & Sastre (1975) the Chilocarpeae are included as a tribe in the Tabernaemontanoideae).

The C a r i s s e a e is generally considered to be one of the most primitive tribes in the family. The group is quite homogeneous. Most are shrubs or woody lianas. In some genera calycine squamellae are present. The anthers are morphologically and histologically unspecialized, but the style-head is morphologically and functionally differentiated into a region of adhesive production and a stigmatic region. Without exception the ovary is congenitally syncarpous and is unilocular or bilocular. The ovary usually has a peripheral layer of tissue that shows a high affinity for safranin. It is supposed that it contains tannins, which reportedly play an important role in preventing premature dispersal of fruits (P. Waterman, pers. comm.). The fruit is a fleshy, indehiscent berry with seeds embedded in a pulp. Dispersal is usually by specialist frugivores (as defined by McKey, 1975).

The P l e i o c a r p e a e show a relationship to the Carisseae by their fleshy, indehiscent (Geissospermum?) berries and flattened, smooth seeds. They are arborescent. Calycine squamellae occur in some of the genera. The corolla tube has slits behind the staminal filaments. The anthers are morphologically and histologically undifferentiated and the pollen is poly-zonocolpate. The style-head is of the first order of complex-

ity, with almost the entire style-head functioning both as the stigma and for the production of adhesive for pollen transport. The ovary is apocarpous, and is normally composed of 2 carpels (up to 5 in Pleiocarpa). Dispersal is usually by specialist frugivores. (Dispersal by primates has been reported for Picralima by P. Waterman, pers. comm.). The Pleiocarpeae are here considered to occupy a central position in the evolutionary complex of the family, and to form a direct link with the Plumerieae, and to have a somewhat more distant relationship with the Rauvolfieae and the Cerberoideae.

The Plumerieae are quite heterogeneous. They may be trees, shrubs, lianas, or herbs. Calycine squamellae are typically absent. The anthers are unspecialized. Both Level 1 and Level 2 style-heads occur. The fruit is composed of two dry follicles; the seeds are typically winged and wind-dispersed.

The Rauvolfieae are trees or shrubs. Calycine squamellae are absent. The anthers are morphologically and histologically unspecialized. The style-head may be of Level 1 or Level 2. The fruit is a drupe or drupe-like, with general tendencies toward partial congenital syncarpy at the base of the ovary, abortion of one carpel, and dispersal by water or frugivores.

Allamanda, the sole member of the tribe Allamandaeae has anthers that are morphologically differentiated in a peculiar way. The dorsal side of the anther is modified into broad side wings with caudate basal appendages. However, the side wings are not sclerenchymatic. The style-head is morphologically and histologically differentiated into an upper region for pollen presentation, a middle adhesive production zone, and the stigmatic region on the underside of the basal "collar" (annulus). The style-head is not 5-lobed in the upper part and is essentially different from that of the Tabernaemontanoideae. The developmental pattern of the ovary (postgenital fusion and parietal placentation) and the dry, spiny, valvate capsules show no affinity to any other genus in the family. The seeds are surrounded by a thickened margin. The lightweight fruit is adapted for water dispersal. Allamanda is an isolated element within the Apocynaceae and is in this scheme shown as having budded off from the central complex.

In their floral structure the Ambelanieae show a closer relationship to the Tabernaemontanoideae than to the Plumerioideae: the anthers are massive and are morphologically and histologically differentiated, with the thecae restricted to the distal part; the dorsal side is sclerenchymatic and elaborated into elongate side wings. The structure of the style-head is the same as that in the Tabernaemontanoideae. The upper part is formed by

a 5-lobed crest that is covered by long hairs, but becomes cylindrical at the level of the stigma. The fleshy fruits, however, are indehiscent, and the seeds lack arils (or have only rudimentary arils). As in the Tabernaemontanoideae and the Carisseae, dispersal is typically zoochorous, but secondary adaptations for water dispersal also occur. The Ambelanieae are considered to be a side branch of the Carisseae, which gave rise to the Tabernaemontanoideae (Monachino, 1945a, b; Pichon, 1948a; Boiteau & Sastre, 1975).

The close relationship between the Ambelanieae and Macoubea of the Tabernaemontanoideae has received considerable attention (Ducke, 1922; Markgraf, 1938; Monachino, 1945a, b; Boiteau & Sastre, 1975; Boiteau et al., 1978). Pichon (1948a) included Macoubea as a subtribe within the Ambelanieae, but Boiteau et al. (1975, 1978) later placed it as a separate tribe within the Tabernaemontanoideae due to its rudimentary arils. Based on its floral structure, Ambelania grandiflora belongs in the Tabernaemontanoideae. As more information becomes available on this relatively little known tribe, it may prove desirable to treat the Ambelanieae (including Macoubea) as a primitive tribe of the Tabernaemontanoideae.

There has been a tendency to exclude genera which in many other features clearly show a close relationship to the Tabernaemontanoideae, simply because the fruits are indehiscent or the seeds do not have an aril, in order that all genera "conform" to the homogeneous concept of the subfamily. This is the same sort of reasoning used by Pichon (1948a) to include the Pleiocarpae in the Carisseae. The disadvantages of this sort of single character taxonomy are well known.

The Tabernaemontanoideae are an extremely uniform subfamily characterized by apocarpous, fleshy, dehiscent fruits and seeds with arils. Multiseriate rows of calycine squamellae are typical. Aestivation of the corolla lobes is usually sinistrorse. The anthers are free from the style-head and are morphologically and histologically differentiated, with the pollen producing tissue restricted to the distal end of the anther, and the dorsal side modified into sclerenchymatic side wings. The style-head is of the Level 2 type. Fruit dispersal is typically by specialist frugivores. The Tabernaemontanoideae are distinguished chemically by the presence of advanced indole alkaloids of the ibogan type. The Tabernaemontanoideae are more advanced than the Plumerioideae in both their floral structure as well as their alkaloid chemistry. The Tabernaemontanoideae are most closely related to the tribe Ambelanieae of the Plumerioideae, and both

are treated here as having a common derivation from the Carisseae.

The *Cerberoidae* is the smallest subfamily, with only five genera, but it is very diverse. The subfamily is characterized by the connective of the anther being broadened at the base and caudate at the apex, with the apices of the anthers sometimes fused; the thecae dehisce sublaterally; the corolla tube is equipped with supra- and infrastaminal appendages, the latter of which may be fused to the style-head. Aestivation of the corolla lobes is sinistrorse. The fruit is bicarpellate and drupaceous, and there is a tendency toward partial congenital syncarpy of the lower part of the ovary. Chemically, the Cerberoideae is separated from the Plumerioideae by the presence of monoterpenes and the absence of indole alkaloids.

The Cerberoideae is considered to be more advanced than the Plumerioideae. I suppose: 1. that this subfamily has originated from Plumerioid ancestors with fruits which developed adaptations for sea water dispersal, 2. that this represented crossing an adaptive threshold, making available a new ecologic niche, and 3. was followed by a subsequent radiation. *Kopsia* and *Ochrosia* (including *Neisosperma*) are considered to be the surviving links. Both of these genera show a pattern of species radiation associated with adaptations for sea water dispersal. Recently a new alkaloid, Kopsirachin, has been isolated from one of the more advanced species of *Kopsia* (K. Homberger & M. Hesse, unpub. results). This is not an indole alkaloid, which are typical for the Plumerioideae, but is a modification of the monoterpene Skytanthine, which has been isolated from the Cerberoid genus *Skytanthus* for some time. This is the first report of a non-indole alkaloid being isolated from a member of the Plumerioideae, and provides strong support for the hypothesis that *Kopsia* is a link between the Plumerioideae and the Cerberoideae.

Cerbera and *Cerberiopsis* still show fruits adapted to sea water dispersal, and thus are considered primitive. The bright red, fleshy fruit of *Thevetia* (including *Cascabela*), on the other hand, is considered to represent secondary adaptations for dispersal by specialist frugivores. The derived fruit characters of *Thevetia* are correlated with a more complex floral structure. Whereas in *Cerbera* and *Cerberiopsis* the stigmatic region is continuous and the infrastaminal appendages may press against the style-head at this level, in *Thevetia* the stigmatic region is interrupted into 10 invaginations of the style-head, with the infrastaminal appendages protruding into five of them and fusing postgenitally with the style-head (see Fig. 16b).

The Apocynoideae is the most advanced subfamily. The majority of the genera are lianas. A reduced number of calycine squamellae are present. Aestivation of the corolla lobes is usually dextrorse. There is a tendency in advanced species for the corolla to be subrotate, with the anthers exserted. The anthers are morphologically and histologically differentiated with the dorsal side elaborated into sclerenchymatic side wings with basal appendages. The ventral side is specialized for pollen production in the distal part, while the lower part develops special hairs that are cemented to the style-head by adhesive secreted by the style-head, forming a gynostegium. The side wings of the anthers are often agglutinated to one another, and there may be postgenital fusion of the staminal filaments with each other. In some advanced genera the hairs on the ventral face of the anther secrete the adhesive which holds them to the style-head. In species in which the anthers are exserted, the anthers may be of a contrasting color to the corolla (e.g., Stephanostema) and function as visual attraction organs. The style-head is morphologically and functionally differentiated and synorganized with the surrounding cone of anthers, forming an upper pollen chamber, a middle adhesive-producing zone, and with the stigma usually restricted to the underside of the style-head (Schick, 1982). A pollen-trapping annulus may or may not be present at the base. The ovary is bicarpellate and is apocarpous except in a few special cases (e.g., Parsonsia), in which the entire gynoecium fuses postgenitally. The fruit is typically composed of two follicles with dry, comose, wind-dispersed seeds. The Apocynoideae lack indole alkaloids, but characteristically contain steroidal alkaloids. In contrast to the heterogeneous Plumerioideae (which also contain over 600 species), the Apocynoideae are very uniform. Presumably this is due to rapid speciation which took place following the appearance of the gynostegium. This means that tribal delimitation in the Apocynoideae is based on rather minor characters. For example, Pichon (1948d) bases the tribes solely on the nature of the hairs on the ventral face of the anther. I find this character difficult to apply and, therefore, I have not attempted to delimit tribes within the Apocynoideae.

7. Summary.

1. Flowers fixed in FAA of 67 species of Apocynaceae and 4 species of Asclepiadaceae comprising 55 and 4 genera respectively, were studied morphologically and anatomically.
2. The floral structure of 18 selected genera, which represent basic evolutionary trends in the Apocynaceae is described. Morphological, anatomical and functional aspects are explained.
3. There is a general trend in the family from congenital syncarpy to secondary apocarpy accompanied by the retention of a compitum formed by the postgenital fusion of the carpel apices. The importance of distinguishing between congenital and postgenital syncarpy is emphasized.
4. There is a general trend from endozoochorous dispersal by specialist frugivores to wind dispersal (which is correlated with the trend from syncarpy to apocarpy). Features of the fruit and seed are shown to be useful taxonomic characters, but have often been given too much weight in previous treatments; such single character taxonomy is shown to be unacceptable.
5. Four basic style-head types are described, based on morphological, histological, and functional complexity.
6. The association of the stigmatic region with the pollen-trapping apparatus is reported, and this is used to demonstrate the trend for this function to be shifted from the style-head to the anthers. The function of the free apices of the style-head is discussed.
7. Basic evolutionary trends of the anthers are presented and four levels of complexity are described. The importance of histological characters is demonstrated. The presence of sclerenchyma is shown to be a derived condition. The position of the sclerenchymatous tissue is a useful taxonomic character. Functional aspects of the tufts of hairs on the ventral face of the anther show the increasing role they play in trapping foreign pollen in the Level 3 and Level 4 type style-head. Adhesive-secreting anthers in two genera of the Apocynoideae are reported for the first time.
8. New morphological evidence is presented which indicates that phylogenetic relationships are better reflected by removing the Pleiocarpaceae from the Carisseae and treating them as a tribe within the Plumerioideae. This tribe should include the problematic genus Geissospermum. This is also supported by chemical characters. Intergeneric relationships are discussed for the Pleiocarpaceae with members of the Plumerieae.
9. The ontogenetic development of the gynoecium of Allamanda is described for the first time, showing that the unilocular ovary is postgenitally syn-

carpous, illustrating a type of gynoecial development not previously known to occur in the Apocynaceae, and supporting an isolated position for Allamanda within the Plumerioideae.

10. In the genus Holarrhena adnation of the stamens to the style-head is shown for the first time, which, together with the body of accumulated morphological and chemical evidence, is used to support its placement in the Apocynoideae.

11. Intergeneric relationships and the evolution of the Cerberoideae are discussed. Kopsia and Ochrosia are suggested as ancestral links between the Plumerioideae and the Cerberoideae, which is also supported by chemical characters.

8. Zusammenfassung.

1. In FAA fixierte Vertreter der Apocynaceae (67 Arten aus 55 Gattungen) und Asclepiadaceae (4 Arten aus 4 Gattungen) wurden morphologisch und anatomisch untersucht.
2. Wichtige Evolutionstendenzen in der Blütenstruktur der Apocynaceae werden anhand von 18 ausgewählten Gattungen beschrieben; dabei werden morphologische, anatomische, und funktionelle Aspekte berücksichtigt.
3. Im Gynoecium besteht eine allgemeine Evolutionstendenz von congenitaler Synkarpie zu sekundärer Apokarpie. Das Compitum bleibt durch postgenitale Verwachsung der Karpellspitzen erhalten. Es wird auf die Bedeutung des Unterschiedes zwischen congenitaler und postgenitaler Synkarpie hingewiesen.
4. In der Verbreitung zeigt sich eine allgemeine Tendenz von der Endozoochorie durch spezialisierte Frugivoren zur Anemochorie. Dies ist korreliert mit dem Trend zur Apokarpie. Es wird gezeigt, dass die Frucht als taxonomisches Merkmal zwar nützlich ist, in ihrer Bedeutung aber oft überschätzt worden ist. Taxonomie anhand nur eines einzelnen Merkmals führt nicht zu befriedigenden Ergebnissen.
5. Aufgrund ihrer verschiedenen Komplexität in morphologischer, histologischer und funktioneller Hinsicht werden vier Narbenkopftypen unterschieden.
6. Narbe und Pollensammelvorrichtung sind immer in bestimmter Beziehung topographisch miteinander korreliert. Dabei kann gezeigt werden, dass evolutiv die Pollenauffangvorrichtung vom Narbenkopf auf die Antheren übertragen wird. Die Funktion der freien Spitzen des Narbenkopfes wird diskutiert.
7. Es werden hauptsächliche Evolutionsrichtungen im Androecium beschrieben. Die Bedeutung histologischer Merkmale wird gezeigt. Das Vorhandensein von Sklerenchym ist hier ein abgeleitetes Merkmal. Die Lage des sklerenchymatischen Gewebes ist als Merkmal für die Taxonomie nützlich. Beim abgeleiteten Narbenkopf (Typ 3) spielen die Haarbüschel auf den Ventralseiten der Antheren eine zunehmend wichtige Rolle bei der Uebertragung von fremdem Pollen. In zwei Gattungen der Apocynoideae werden erstmals klebstoffsezernierende Antheren beschrieben.
8. Die Ergebnisse der morphologischen Untersuchungen zeigen, dass die Pleiocarpinae aus den Carisseae genommen und als Tribus in die Plumerioideae gestellt werden sollten. Diese Tribus sollte auch die problematische Gattung Geissospermum einschliessen - dafür sprechen auch chemische Merkmale. Ver-

wandtschaftsbeziehungen zwischen Gattungen der Pleiocarpeae und Vertretern der Plumerieae werden diskutiert.

9. Die Ontogenese des Gynoeciums von Allamanda wird erstmals beschrieben. Sie zeigt, dass das einfächrige Ovar postgenital synkarp ist. Diese Art der Gynoeciumentwicklung war bisher bei den Apocynaceae noch unbekannt. Sie bestätigt die angenommene Sonderstellung von Allamanda unter den Plumerioideae.

10. Bei der Gattung Holarrhena konnte zum ersten Mal die Verbindung zwischen Stamina und Narbenkopf gezeigt werden. Sie spricht, zusammen mit andern morphologischen und chemischen Argumenten, für die Stellung von Holarrhena bei den Apocynoideae, und nicht den Plumerioideae.

11. Verwandtschaftsbeziehungen und Evolutionstendenzen bei Gattungen der Cerberoideae werden diskutiert. Es wird angenommen, dass Kopsia und Ochrosia phylogenetische Verbindungsglieder zwischen den Plumerioideae und den Cerberoideae darstellen. Für diese Stellung sprechen auch chemische Merkmale.

9. Literature Cited.

- Allorge, L. 1975. Rattachement de la tribu des Allamandées aux Echitoidées (Apocynacées). *Adansonia*, ser. 2, 15: 273-276.
- _____. 1976. Morphologie et biologie florale des Apocynacées, applications taxonomiques. Thèse, Ecole Pratique des Hautes Etudes. Paris. 113 pp.
- _____, H.P. Husson & C. Sastre. 1980. Morphologie et chimiotaxonomie des Apocynacées, conclusions phylogénétiques et biogéographiques. *Compt. Rend. Commaire Séances Soc. Biogéogr.* 57: 112-126.
- Andersson, A. 1931. Studien über die Embryologie der Familien Celastraceae, Oleaceae und Apocynaceae. *Acta Univ. Lund.*, n.s. 27(7): 1-110.
- Baillon, H. 1891. *Histoire des Plantes* 10: 146-218. Paris.
- Baum, H. 1949. Die Stellung der Samenanlagen am Karpell bei *Asclepias syriaca*, *Cynanchum vincetoxicum* und *Erythraea centaurium*. *Oesterr. Bot. Z.* 95: 251-256.
- _____. 1953. Die Unabhängigkeit der diplophyllen Gestalt der Staubblattspreite von ihrer Funktion als Träger der Pollensäcke. *Oesterr. Bot. Z.* 100: 265-269.
- Beentje, H.J. 1978. A revision of *Callichilia* Stapf (Apocynaceae). *Meded. Landbouwhoges. Wageningen* 78(7): 1-32.
- Bentham, G. & J.D. Hooker. 1876. *Genera plantarum* 2: 681-728.
- Bisset, N.G. 1981. Phytochemistry of *Holarrhena* R. Br. *Meded. Landbouwhoges. Wageningen* 81(2): 37.
- Boiteau, P. 1975. La ségrégation chimique, marque de l'archaïsme des taxons d'origine gondwanienne (étude des alcaloïdes indoliques et progrès des connaissances en systématique des Apocynacées). *Boissiera* 24: 363-367.
- _____. 1977. Bases méthodologiques du classement des Tabernaemontanoideae (Apocynaceae). *Adansonia*, ser. 2, 17: 235-241.
- _____. 1981. Apocynacées, in: Aubréville, A. & J.-F. Leroy (Eds.). *Flore de la Nouvelle Calédonie et dépendances* 10. *Mus. Natl. Hist. Nat.*, Paris.
- _____ & L. Allorge. 1978. Morphologie et biologie florales des Apocynacées: I. Différences essentielles entre les Plumérioidées et les Tabernaemontanoïdées. *Adansonia*, ser. 2, 17: 305-326.
- _____, _____ & C. Sastre. 1978. Morphologie florale des Apocynaceae: II. Caractères distinctifs entre Ambelanieae (Plumerioideae) et Macoubeae (Tabernaemontanoideae). *Adansonia*, ser. 2, 18: 267-277.
- _____ & C. Sastre. 1975. Sur l'arille des *Macoubea* et la classification de la sous-famille des Tabernaemontanoïdées (Apocynacées). *Adansonia*, ser. 2, 15: 239-250.

- Boke, N.H. 1948. Development of the perianth in Vinca rosea L. Amer. J. Bot. 35: 413-423.
- _____. 1949. Development of the stamens and carpels in Vinca rosea L. Amer. J. Bot. 36: 535-547.
- Candolle, A.P. de. 1844. Prodrum systematis naturalis regni vegetabilis 8: 317-489. Paris.
- Carr, S.G.M. & D.J. Carr. 1961. The functional significance of syncarpy. Phytomorphol. 11: 249-256.
- Church, A.H. 1908. Types of floral mechanism, Part I, Types I-XII. Oxford.
- Corry, T.H. 1883. On the structure and development of the gynostegium, and the mode of fertilization in Asclepias cornuti Decaisne (A. syriaca L.). Trans. Linn. Soc. London 2, ser. 2: 173-207, pl. 24-26.
- De Jong, B.H.J. 1979. A revision of the African species of Alstonia R. Br. (Apocynaceae). Meded. Landbouwhoges. Wageningen 79(13): 1-16.
- De Kruif, A.P.M. 1981. A revision of Holarrhena R. Br. (Apocynaceae). Meded. Landbouwhoges. Wageningen 81(2): 1-36.
- Delpino, F. 1867. Sugli apparecchi della fecondazione nelle piante antocarpee (Fanerogame). Sommario di osservazione fatte negli anni 1865-1866. Firenze.
- Demeter, K. 1922. Vergleichende Asclepiadaceenstudien. Flora 115: 130-176.
- Ducke, A. 1922. Plantes nouvelles ou peu connues de la région amazonienne. Apocynaceae. Arch. Jard. Bot. Rio de Janeiro 3: 239-248.
- Endress, P.K. 1979. Noncarpellary pollination and "hyperstigma" in an angiosperm (Tambourissa religiosa, Monimiaceae). Experientia 35: 45.
- _____. 1980. Ontogeny, function and evolution of extreme floral construction in Monimiaceae. Pl. Syst. Evol. 234: 79-120.
- _____. 1982. Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive angiosperms. Taxon 31: 48-52.
- _____, M. Jenny & M.E. Fallen. In press. Convergent elaboration of apocarpous gynoecea in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). Nord. J. Bot.
- Ezcurra, C. 1981. Revisión de las Apocináceas de la Argentina. Darwiniana 23: 367-474.
- Fallen, M.E. In press. A systematic revision of Anechites (Apocynaceae). Brittonia.
- French, R.C. 1883. Insects caught by Apocynum. Bot. Gaz. 8: 171-172.
- Frye, T.C. & E.R. Blodgett. 1905. A contribution of the life history of Apocynum androsaemifolium. Bot. Gaz. 40: 49-53.
- Ganzinger, D. & M. Hesse. 1976. A chemotaxonomic study of the subfamily

- Plumerioideae of the Apocynaceae. *Lloydia* 39: 326-349.
- Gensel, W.H. 1969. A revision of the genus Thevetia (Apocynaceae). Unpublished Masters Thesis, The University of Connecticut. Storrs. 143 pp.
- Gut, B.J. 1966. Beiträge zur Morphologie des Gynoeceums und der Blütenachse einiger Rutaceen. *Bot. Jahr. Syst.* 85: 151-247.
- Hickey, M. & C.J. King. 1981. 100 families of flowering plants. Cambridge.
- Hildebrand, F. 1867. Federigo Delpinos Beobachtungen über die Bestäubungsvorrichtungen bei den Phanerogamen. Mit Zusätzen und Illustrationen. *Bot. Zeitung* 28: 265-287.
- Kisakürek, M.V., A.J.M. Leeuwenberg & M. Hesse. 1983. A chemotaxonomic investigation of the plant families of Apocynaceae, Loganiaceae, and Rubiaceae by their indole alkaloid content. In: Pelletier, S.W. (Ed.). *Alkaloids: Chemical and Biological Perspectives* 1: 211-376. In press.
- Kunze, H. 1982. Morphogenese und Synorganisation des Bestäubungsapparates einiger Asclepiadaceen. *Beitr. Biol. Pflanzen* 56: 133-170.
- Kupicha, F.K. 1981. Studies on African Apocynaceae: two new taxa in Alafia Thours. *Bull. Jard. Bot. Nat. Belg.* 51: 153-163.
- Leeuwenberg, A.J.M. 1980. The taxonomic position of some genera in the Loganiaceae, Apocynaceae, and Rubiaceae, related families which contain alkaloids. In: Phillipson, J.D. & M.H. Zenk (Eds.). *Indole and biogenetically related alkaloids*. *Ann. Proc. Phytochem. Soc. Europe* 17: 1-10.
- Leinfellner, W. 1951. Die Nachahmung der durch kongenitale Verwachsung entstandenen Formen des Gynözeums durch postgenitale Verschmelzungsvorgänge. *Oesterr. Bot. Z.* 98: 403-411.
- Léon, H. & H. Alain. 1957. *Flora de Cuba* 4: 170-197. La Habana.
- Lippold, H. 1980. Die Gattungen Thevetia L., Cerbera L. und Cascabela Rafin. (Apocynaceae). *Feddes Repert.* 91: 45-55.
- Ludwig, F. 1880. Ueber die Bestäubungsvorrichtungen und die Fliegenfalle des Hundsköhles, Apocynum androsaemifolium L. *Kosmos* 8: 182-185.
- McCoy, R.W. 1940. Floral organogenesis in Frasera carolinensis. *Amer. J. Bot.* 27: 600-609.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. In: Gilbert, L. & P.H. Raven (Eds.). *Coevolution of animals and plants*. Austin and London.
- Markgraf, F. 1938. Die amerikanischen Tabernaemontanoideen. *Notizbl. Bot. Gart. Berlin-Dahlem* 14: 151-184.
- . 1972. *Florae Malesianae Praecursores* LIII. Apocynaceae II. *Blumea* 20: 407-425.

- _____. 1974. Morphologische Kleinigkeiten mit grösseren Folgen. *Phyton* (Austria) 16: 105-116.
- _____ & K. Huber. 1975. Die Entwicklung der "Nasefrucht" von *Kopsia flavida* Bl. Bot. Jahrb. Syst. 96: 256-269.
- Marques, M. & T.S. Melhem. 1966. Pollen grains of plants of the "cerrado". II, Apocynaceae. *Anais Acad. Bras. Cienc.* 38: 371-378.
- Mayr, E. 1979. Animal species and evolution. Cambridge, Mass.
- Miers, J. 1878. On the Apocynaceae of South America. Edinburgh and London.
- Monachino, J. 1945a. A revision of *Ambelania*, inclusive of *Neocouma* (Apocynaceae). *Lloydia* 8: 109-130.
- _____. 1945b. A revision of *Macoubea* and the American species of *Landolphia* (Apocynaceae). *Lloydia* 8: 291-317.
- Müller-Argoviensis, J. 1860. Apocynaceae. In: Martius, C. (Ed.). *Flora Brasiliensis* 6(1): 1-196.
- Ngan, P.T. 1965. A revision of the genus *Wrightia* (Apocynaceae). *Ann. Missouri Bot. Gard.* 52: 114-175.
- Nishino, E. 1982. Corolla tube formation in six species of Apocynaceae. *Bot. Mag. Tokyo* 95: 1-17.
- Padmanabhan, D., D. Regupathy & S. Pushpa Veni. 1978. Gynoecial ontogeny in *Enicostemma littorale* Blume. *Proc. Ind. Acad. Sci., B*, 87: 83-92.
- Pichon, M. 1948a. Classification des Apocynacées. I, Carissées et Ambélianiées. *Mém. Mus. Natl. Hist. Nat.* 24: 111-181.
- _____. 1948b. Classification des Apocynacées. V, Cerberoidées. *Not. Syst.* 13: 212-229.
- _____. 1948c. Classification des Apocynacées. IX, Rauvolfiées, Alstoniées, Allamandées et Tabernémontanoidées. *Mém. Mus. Natl. Hist. Nat.* 27: 153-252.
- _____. 1948d. Classification des Apocynacées. XIX, Le rétinacle des Echitoidées. *Bull. Soc. Bot. France* 95: 211-216.
- _____. 1950. Classification des Apocynacées. XXV, Echitoidées et XXVIII, Suppl. aux Plumérioidées. *Mém. Mus. Natl. Nat., Sér. B, Bot.* 1: 1-174.
- _____. 1952. Classification des Apocynacées. XXXIII, Les Sous-tribus des Carissées. *Not. Syst.* 14: 310-315.
- _____. 1953a. Monographie des Landolphiées. Classification des Apocynacées. XXXV. *Mém. Inst. Franc. Afrique Noire* 35: 1-437.
- _____. 1953b. Classification des Apocynacées. XXXVI, Révision des Pleiocarpinées. *Bol. Soc. Brot., 2 sér.* 27: 73-153.
- Prance, G.T. & S.A. Mori. 1978. Observations on the fruits and seeds of neotropical Lecythidaceae. *Brittonia* 30: 21-33.

- Radford, A.E., W.C. Dickison, J.R. Massey & C.R. Bell. 1974. Vascular plant systematics. New York.
- Rao, A.S. 1956. A revision of Rauvolfia with particular reference to the American species. Ann. Missouri Bot. Gard. 43: 253-355.
- Rowley, G.D. 1980. The pollination mechanism of Adenium (Apocynaceae). Nat. Cactus and Succ. Journal 35: 2-5.
- Safwat, F. 1962. The floral morphology of Secamone and the evolution of the pollinating apparatus in Asclepiadaceae. Ann. Missouri Bot. Gard. 49: 95-129.
- Schick, B. 1980. Untersuchungen über die Biotechnik der Apocynaceenblüte. I. Morphologie und Funktion des Narbenkopfes. Flora 170: 394-432.
- _____. 1982. Untersuchungen über die Biotechnik der Apocynaceenblüte. II. Bau und Funktion des Bestäubungsapparates. Flora 172: 347-371.
- Schmid, R. 1976. Filament histology and anther dehiscence. Bot. J. Linn. Soc. (London) 73: 303-315.
- Schumann, K. 1895. Apocynaceae. In: Engler, A. & K. Prantl (Eds.). Die natürlichen Pflanzenfamilien 4(2): 109-189. Leipzig.
- Sprengel, C.K. 1793. Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Berlin.
- Stapf, O. 1902. Apocynaceae. In: Thiselton-Dyer, W.T. (Ed.). Flora of Tropical Africa 4: 24-231. London.
- Stebbins, G.L. 1974. Flowering plants: Evolution above the species level. Cambridge, Mass.
- Stiles, F.G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. Ann. Missouri Bot. Gard. 68: 323-351.
- Vijayaraghavan, M.R. & U. Padmanaban. 1969. Morphology and embryology of Centaurium ramosissimum Druce and affinities of the family Gentianaceae. Beitr. Biol. Pfl. 46: 15-37.
- Wagenitz, G. 1964. Gentianales. In: Melchior, H. (Ed.). Engler's Syllabus der Pflanzenfamilien, ed. 12, 2: 403-424. Berlin.
- Walker, D.B. 1975. Postgenital carpel fusion in Catharanthus roseus (Apocynaceae). I. Light and scanning electron microscopic study of gynoecial ontogeny. Amer. J. Bot. 64: 457-467.
- _____. 1978. Postgenital carpel fusion in Catharanthus roseus (Apocynaceae). IV. Significance of the fusion. Amer. J. Bot. 65: 119-121.
- Woodson, R.E., Jr. 1930. Studies in the Apocynaceae I. A critical study of the Apocynoideae (with special reference to the genus Apocynum). Ann. Missouri Bot. Gard. 17: 1-212.

- _____. 1933, 1935, 1936. Studies in the Apocynaceae IV. The American genera of Echitoideae. Ann. Missouri Bot. Gard. 20: 605-790; 22: 153-306; 23: 169-438.
- _____. 1951. Studies in the Apocynaceae VIII. An interim revision of the genus Aspidosperma Mart. & Zucc. Ann. Missouri Bot. Gard. 38: 119-206.
- Zwetsloot, H.J.C. 1981. A revision of Farquharia Stapf and Funtumia Stapf (Apocynaceae). Meded. Landbouwhoges. Wageningen 81(16): 1-46.

10. Figure Captions.

Symbols used are as follows:

- Adhesive (secretion) - small stippling
- Stigmatic and transmitting tissue - large stippling
- Postgenitally fused areas - dashed lines
- Sclerenchyma - black

(In the transverse sections the calyx is not drawn).

Fig. 1-2. Aspidosperma pyricollum.--Flower at anthesis; 1, partially schematic longitudinal section; 2, transverse section series; a, upper region of the anthers; b, gaps in the corolla tube just above the juncture of the staminal filaments; c, stigmatic region of style-head; d, style with central cylinder of transmitting tissue; e, ovary.

Fig. 3-4. Pleiocarpa mutica.--Flower at anthesis; 3, partially schematic longitudinal section; 4, transverse section series; a, upper region of the anthers; gaps in the corolla tube just above the juncture of the staminal filaments; c, stigmatic region of the style-head with five divisions of the style-head still distinguishable; d, level of the style with more or less hollow central region; e, ovary.

Fig. 5-6. Geissospermum laeve.--Flower at anthesis; 5, partially schematic longitudinal section; 6, transverse section series; a, level of the anthers; b, level at which gaps occur in the corolla tube behind the staminal filaments; c, stigmatic region of the style-head; d, carpels surrounded by many lignified hairs.

Fig. 7-8. Haplophyton crooksii.--Flower at anthesis; 7, partially schematic longitudinal section; 8, transverse section series; a, upper region of the anthers; b, level where the staminal filaments begin to separate from the anthers, with gaps in the corolla tube; c, stigmatic region of the style-head; d, ovary.

Fig. 9-10. Landolphia owariensis.--Flower at anthesis; 9, partially schematic longitudinal section; 10, transverse section series; a, level at which the anthers begin to separate from the staminal filaments, style-head without secretory epithelium; b, style-head near the base at the level of the stigma; c, style with a central region of transmitting tissue; d, congenitally fused ovary with parietal placentation.

Fig. 11-12. Kopsia fruticosa.--Flower at anthesis; 11, partially schematic longitudinal section; 12, transverse section series; a, level of the anthers; b, level of the staminal filaments and style-head apices; c, adhesive-producing region of the style-head; d, stigmatic region of the style-head; e, style with central column of transmitting tissue; f, ovary with two nectaries.

Fig. 13-14. Neisosperma nakaiana.--Flower at anthesis; 13, partially schematic longitudinal section; 14, transverse section series; a, stamens with sclerenchymatic tissue; b, upper level of the style-head just before the juncture of the staminal filaments with the corolla tube; c, stigmatic region of the style-head; d, style with central column of pollen tube transmitting tissue; e, ovary, upper apocarpous region; f, ovary, congenitally fused lower region.

Fig. 15-16. Thevetia ahouai.--Flower at anthesis; 15, partially schematic longitudinal section; 16, transverse section series; a, anthers and style-head apices; b, style-head showing interrupted stigmatic zone and adnation of the infrastaminal appendages; c, base of the style-head with united pollen tube transmitting tissue; d, ovary with nectary disc partially in view.

Fig. 17-18. Allamanda schottii.--Flower at anthesis; 17, partially schematic longitudinal section; 18, transverse section series; a, upper level of the stamens; b, lower level of the stamens and style-head apices; c, style-head with upper wreath of hairs; d, adhesive-producing region of the style-head; e, stigmatic region of the style-head, under the basal annulus; f, protuberances of the corolla tube, and style with central column of pollen tube transmitting tissue; g, upper region of ovary; h, ovary, showing parietal placentation and nectary disc partially in view.

Fig. 19-20. Callichilia barteri.--Flower at anthesis; 19, partially schematic longitudinal section; 20, transverse section series; a, level of the thecae; b, anthers showing dorsal appendage; c, upper region of the style-head; d, adhesive-producing region of the style-head; e, stigmatic region of the style-head; f, five-sided style with central column of transmitting tissue; g, ovary with most of the lobed nectary disc visible.

Fig. 21-22. Voacanga africana.--Flower at anthesis; 21, partially schematic longitudinal section; 22, transverse section series; a, level of the thecae; b, upper level of the style-head showing five lobes, with surrounding anthers; c, adhesive-secreting zone of the style-head; d, stigmatic region of the style-head showing the close fit of surrounding anthers; e, lower region of the style-head and elongate basal appendages of the anthers; f, style, showing twisted corolla tube; g, ovary.

Fig. 23-24. Wrightia religiosa.--Flower at anthesis; 23, partially schematic longitudinal section; 24, transverse section series; a, upper region of the thecae; b, lower region of the thecae and style-head apices; c, adhesive-producing zone of the style-head showing adhesive filling the space between the style-head and the surrounding anther cone; d, stigmatic region of the style-head with the surrounding anthers attached by tufts of hairs on their ventral face; e, style with pollen tube transmitting tissue around the periphery of a more or less hollow central column, with surrounding cone of anthers showing sclerenchymatic side wings; f, ovary.

Fig. 25-26. Funtumia africana.--Flower at anthesis; 25, partially schematic longitudinal section; 26, transverse section series; a, cone of anthers at the level of the thecae; b, adhesive-producing region of the style-head with adhesive filling the space between the style-head and the surrounding anther cone; c, secretory hairs on the ventral face of the anthers are adnate to the style-head, dividing the corolla tube into five chambers, and style-head showing five stigmatic regions; d, near the base of the style-head showing unified pollen tube transmitting tissue; e, style with central column of pollen tube transmitting tissue; f, ovary surrounded by an annular nectary.

Fig. 27-28. Holarrhena floribunda.--Flower at anthesis; 27, partially schematic longitudinal section; 28, transverse section series; a, anthers at the level of the thecae; b, anthers below the level of the thecae; c, level of the staminal filaments; d, stigmatic region of the style-head with adnate secretory hairs on the staminal filaments; e, ovary.

Fig. 29-30. Prestonia riedelii.--Flower at anthesis; 29, partially schematic longitudinal section; 30, transverse section series; a, upper region of the anther cone showing corolla tube with induplicately folded petals; b, inner pollen sacs with enlarged epidermal cells adnate to the upper region

(apices) of the style-head, forming five "pollen chambers"; c, expanded region of the style-head just below the apices; d, adhesive-producing region of the style-head; e, level of the stigma showing adnation of secretory tufts of hairs on the ventral face of the anthers with the style-head; f, protuberances of staminal filaments with glandular hairs surround the style and divide the corolla tube into five nectar channels; g, ovary with massive, 5-lobed nectary.

Fig. 31-32. Parsonsia capsularis.--Flower at anthesis; 31, partially schematic longitudinal section; 32, transverse section series; a, inner pollen sacs with enlarged epidermal cells are adnate to the upper region of the style-head forming five pollen chambers; b, adhesive-secreting region of the style-head; c, stigmatic region near the base of the style-head with the surrounding anthers adnate by tufts of secretory hairs; d, just below the stigmatic region showing annulus at the base of style-head, anthers connate by the adnation of the outer edges of the tufts of hairs, dividing the corolla tube into a central chamber surrounded by five peripheral chambers; e, postgenitally fused staminal filaments surrounding the style; f, postgenitally fused ovary.

Fig. 33-34. Mandevilla laxa.--Flower at anthesis; 33, partially schematic longitudinal section; 34, transverse section series; a, upper region of the thecae with inner pollen sac walls of adjacent anthers postgenitally fused and outer pollen sac walls of adjacent anthers agglutinated to each other, forming five pollen chambers; b, upper region of the 5-lobed style-head, and anthers below the level of the thecae adnate to the style-head; , middle region of the style-head with ventral faces of the anthers producing adhesive; d, style-head at the level of the stigma; e, basal annulus of the style-head with adnate anthers; f, staminal protuberances surrounding the style; g, ovary with surrounding nectary disc partially in view.

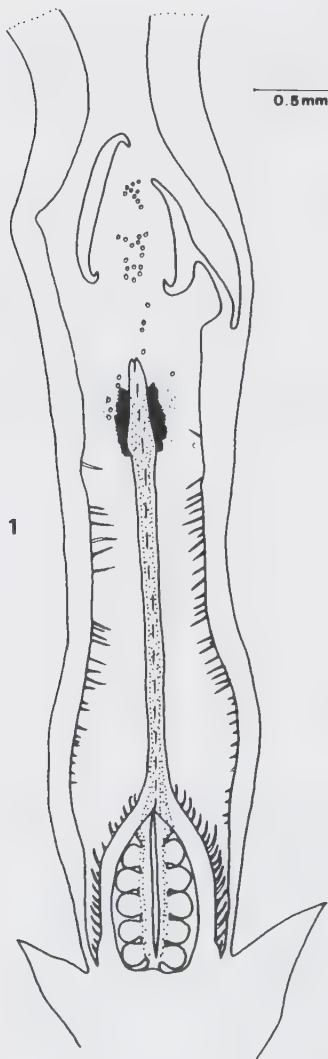
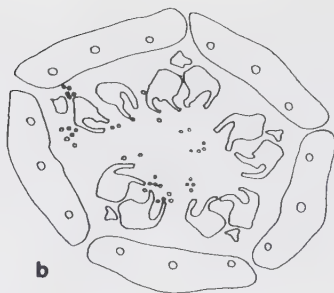
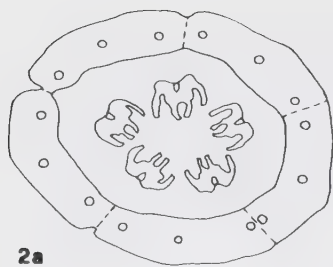
Fig. 35-36. Ambelania grandiflora.--Flower at anthesis; 35, partially schematic longitudinal section; 36, transverse section series; a, anthers at the level of the thecae; b, five-lobed upper region of the style-head with surrounding anthers; c, adhesive-secreting zone of the style-head; d, stigmatic region of the style-head; e, style with pollen tube transmitting tissue in the center; f, unilocular, congenitally fused ovary.

Fig. 37-45. Allamanda schottii.--Gynoecium development; 37-42, SEM micrographs; 37, floral apex with carpel primordia, x 240; 38, the ventral side

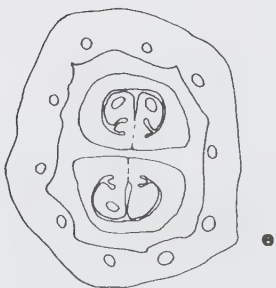
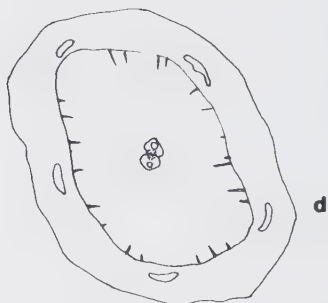
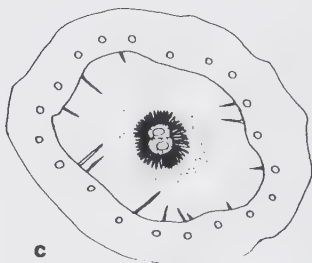
of the carpels become concave, x 190; 39, undifferentiated gynoecium, lobes of nectary disc begin to form, x 190; 40, carpels begin to fuse postgenitally and gynoecium is differentiated into style-head and ovary, x 90; 41, gynoecium of medium-sized bud; a, entire gynoecium, showing advanced morphological differentiation, x 21; b, close-up of the region of fusion of the two carpels, x 190; c, close-up of the style-head showing differentiation of the papillose epidermis, apical appendages, and the basal "collar", x 53; 42, ovary at a later stage, showing a groove along the juncture of the two carpels, x 53; 43-45, transverse sections; 43, ovary of bud in Fig. 38, x 125; 44, ovary of bud in Fig. 29, x 125; 45, gynoecium of Fig. 41; a, style-head with no epidermis visible in the region of fusion between the two carpels, x 125; b, ovary, showing epidermis still distinguishable in the region of fusion between the two carpels, and parietal placentation, x 125.

Fig. 46. Holarrhena pubescens.--Flower at anthesis, longitudinal section, showing adnation of staminal hairs to the style-head, x 50.

Fig. 47. Phylogenetic diagram of the major taxonomic groups of the Apocynaceae. In the diagram the size of the group represents the approximate number of species it contains, while the absolute height at which a group appears is an expression of its evolutionary advancement relative to the other groups.

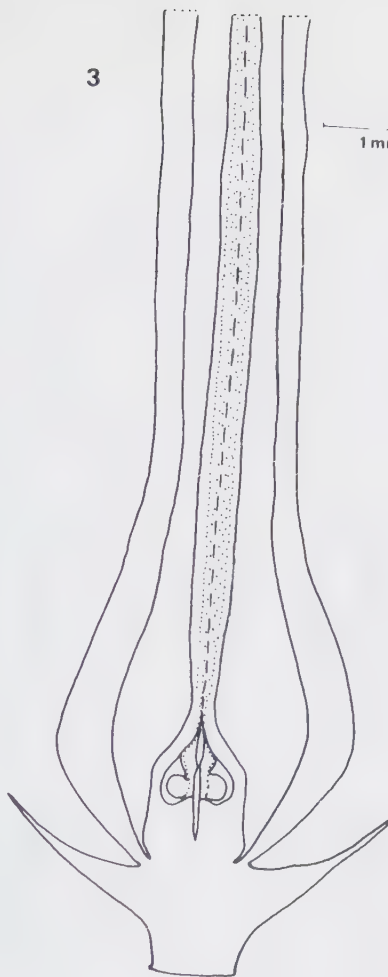


0.5 mm





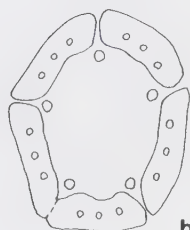
3



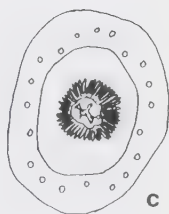
1 mm



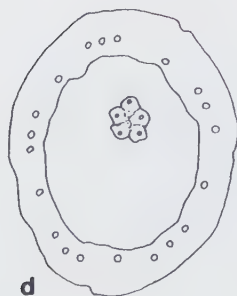
4a



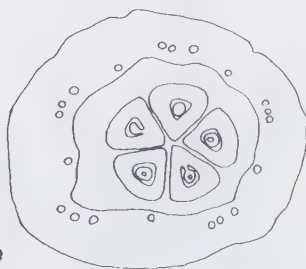
b



c

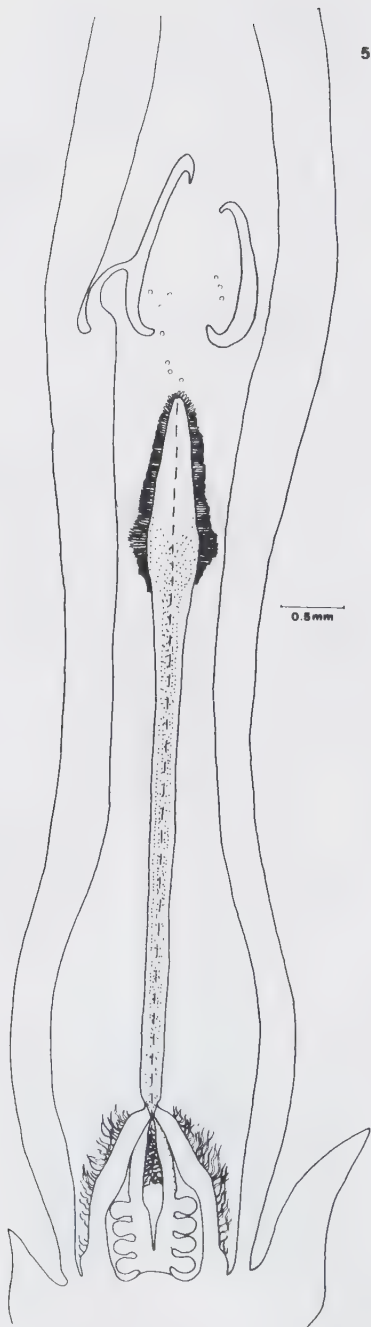


d



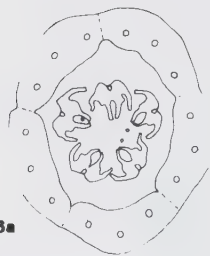
e

5

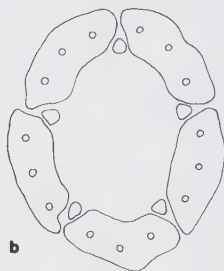


0.5 mm

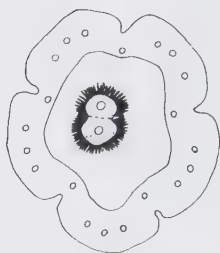
6a



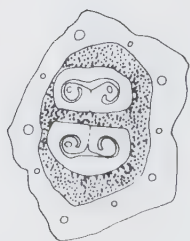
b



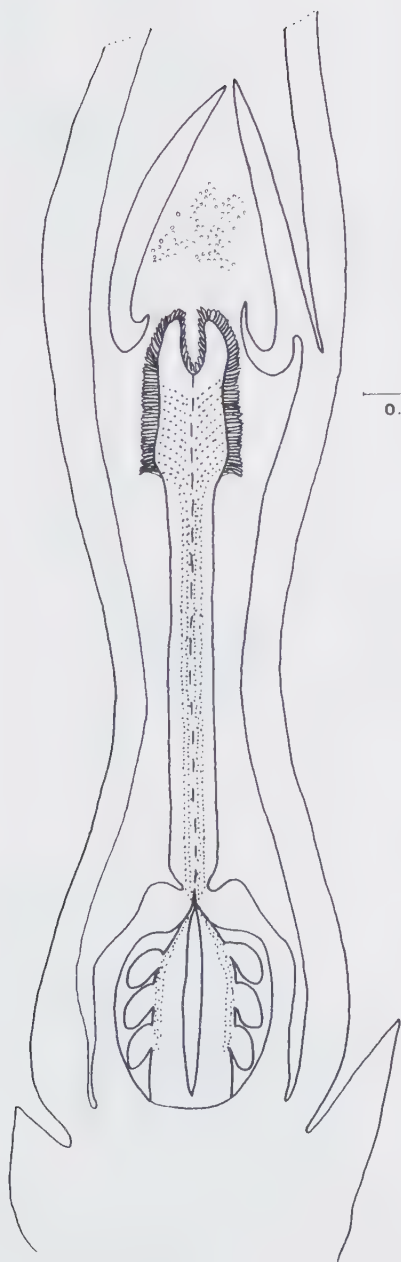
c



d



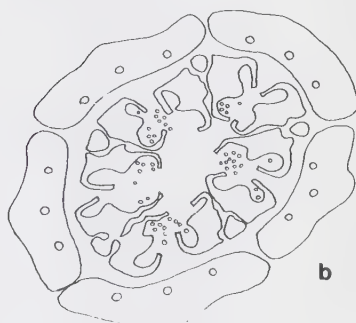
7



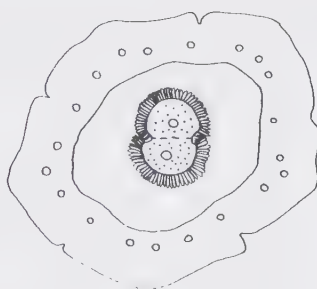
0.5 mm



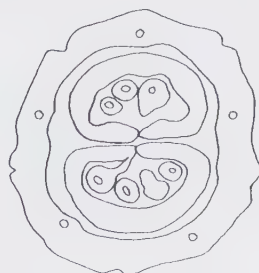
8a



b

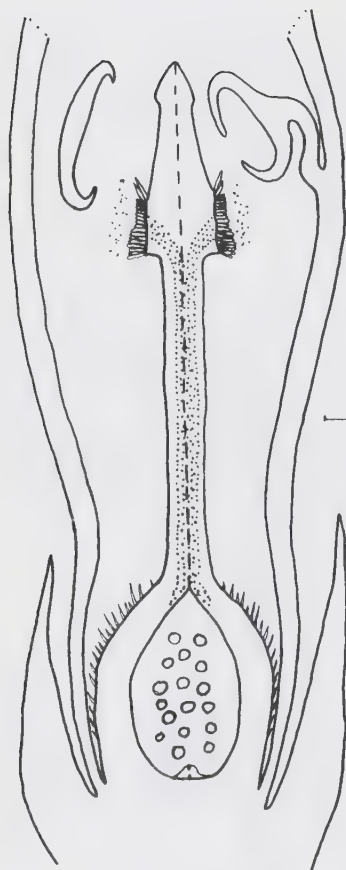


c



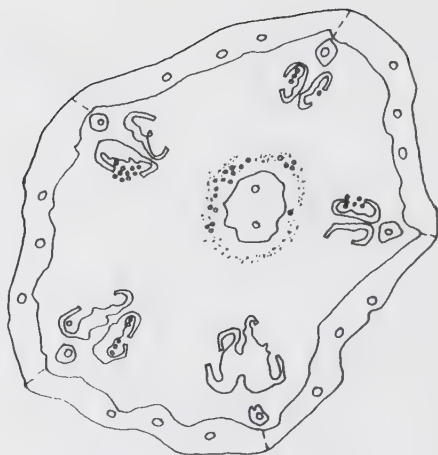
d

9

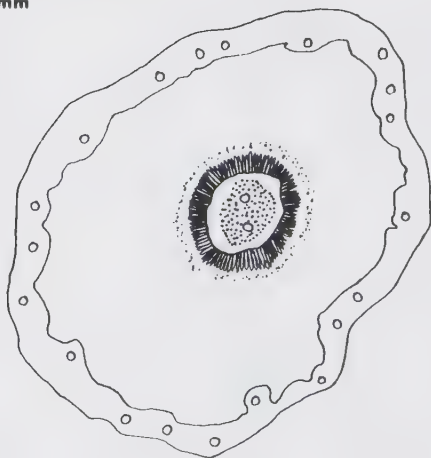


1 mm

10a



b

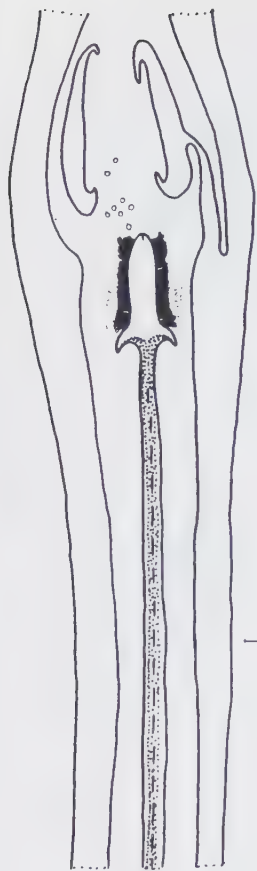


c



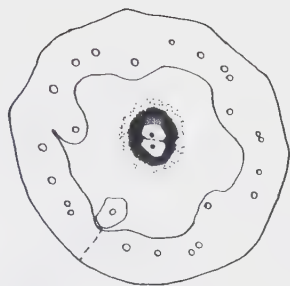
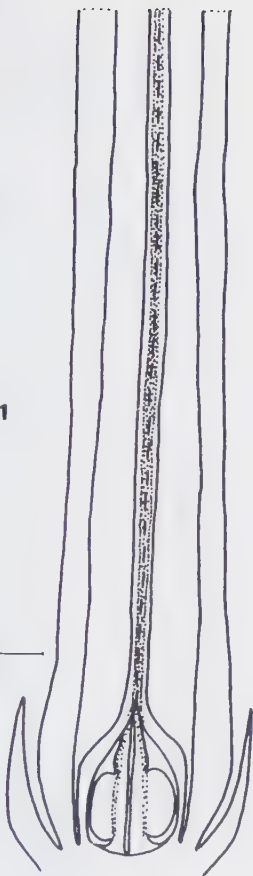
d



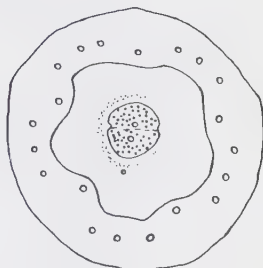


11

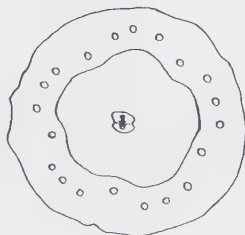
1mm



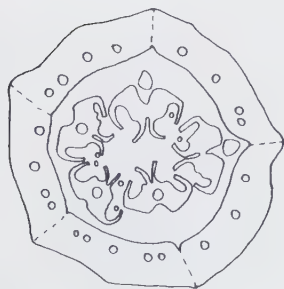
c



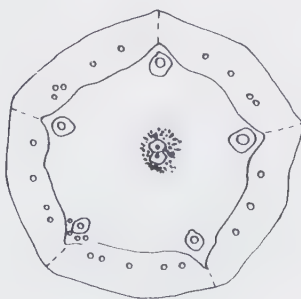
d



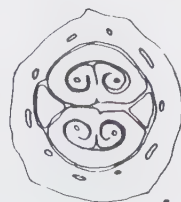
e



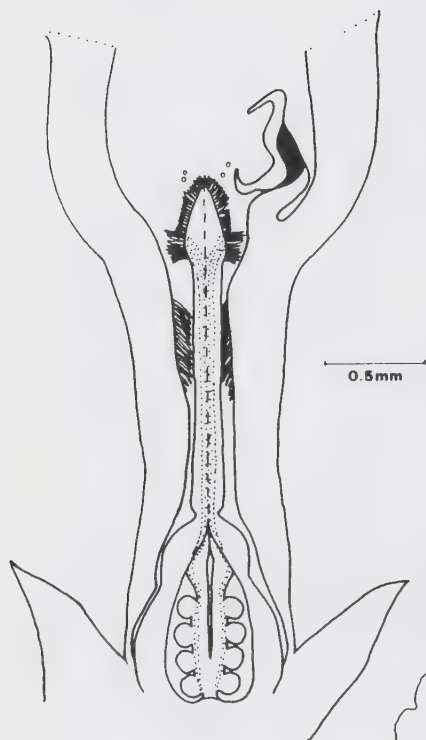
12a



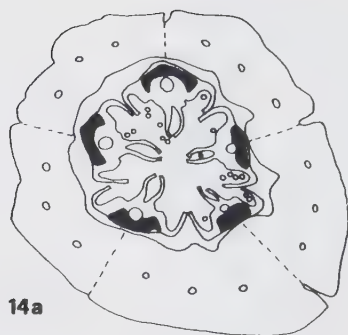
b



f



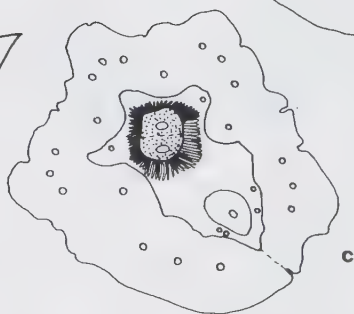
13



14a



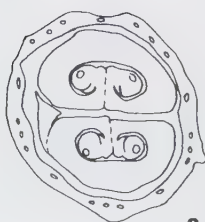
b



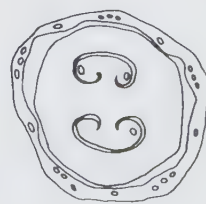
c



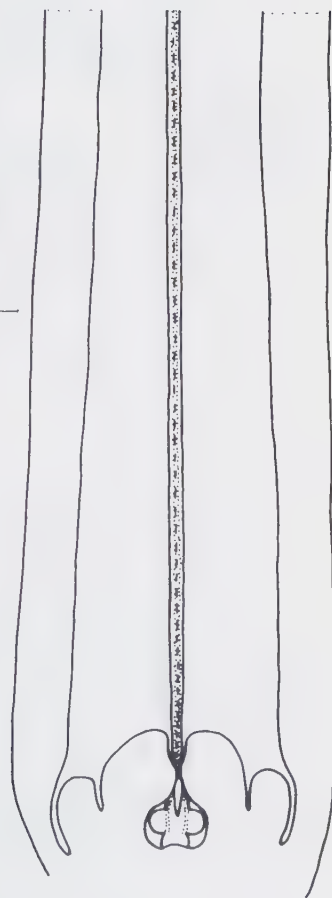
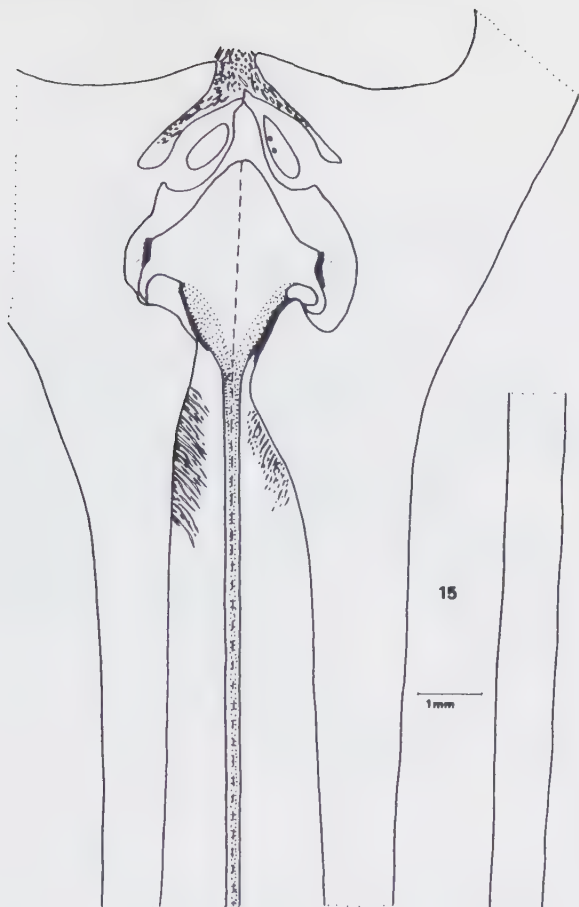
d



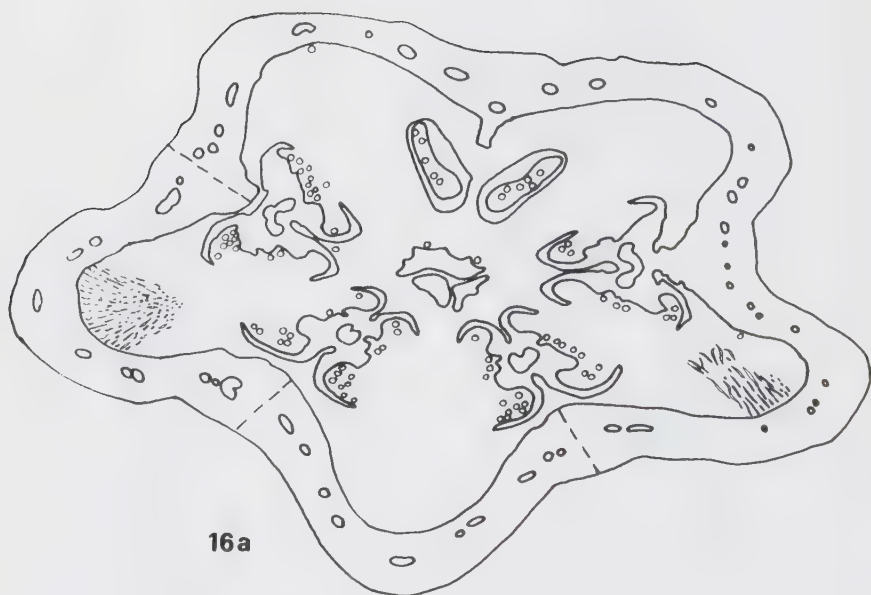
e



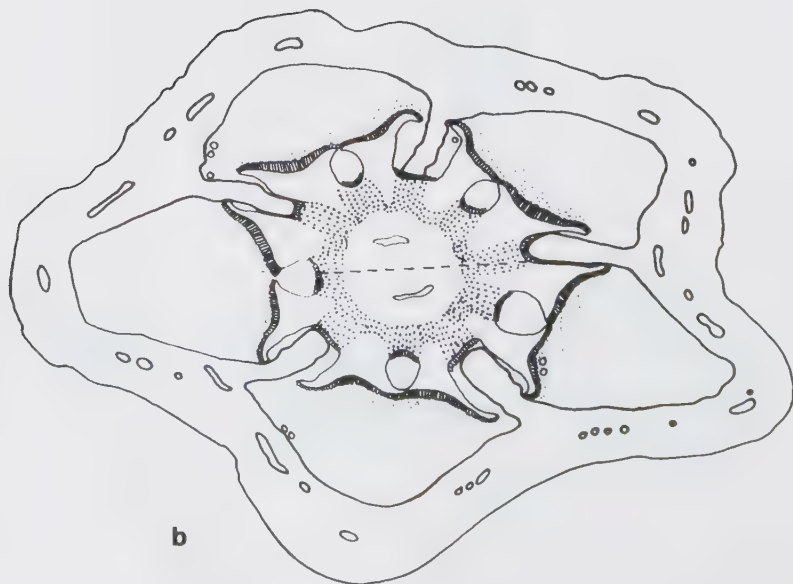
f



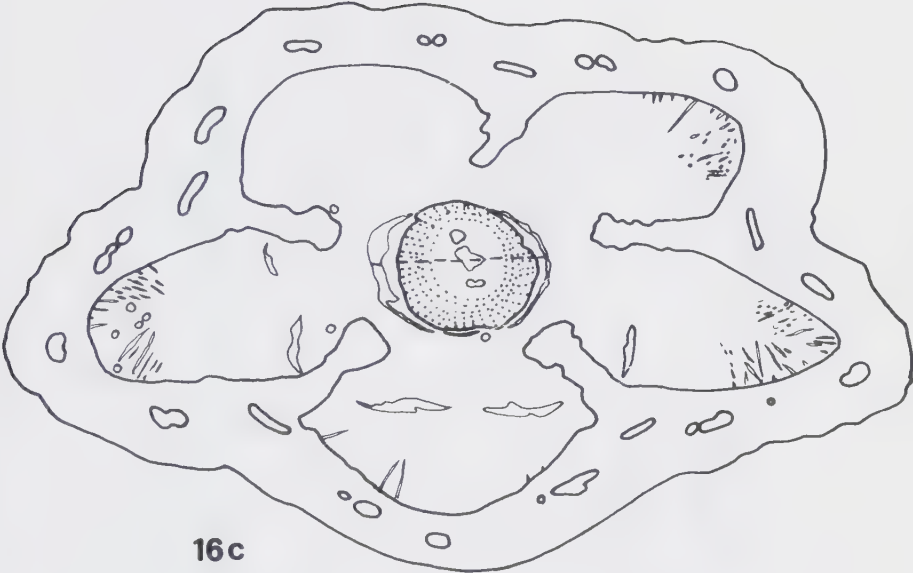
1 mm



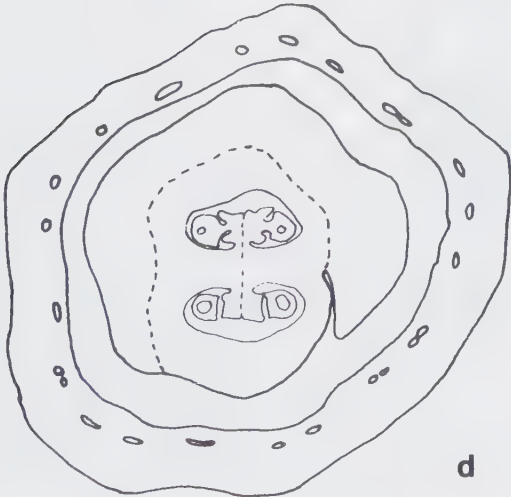
16a



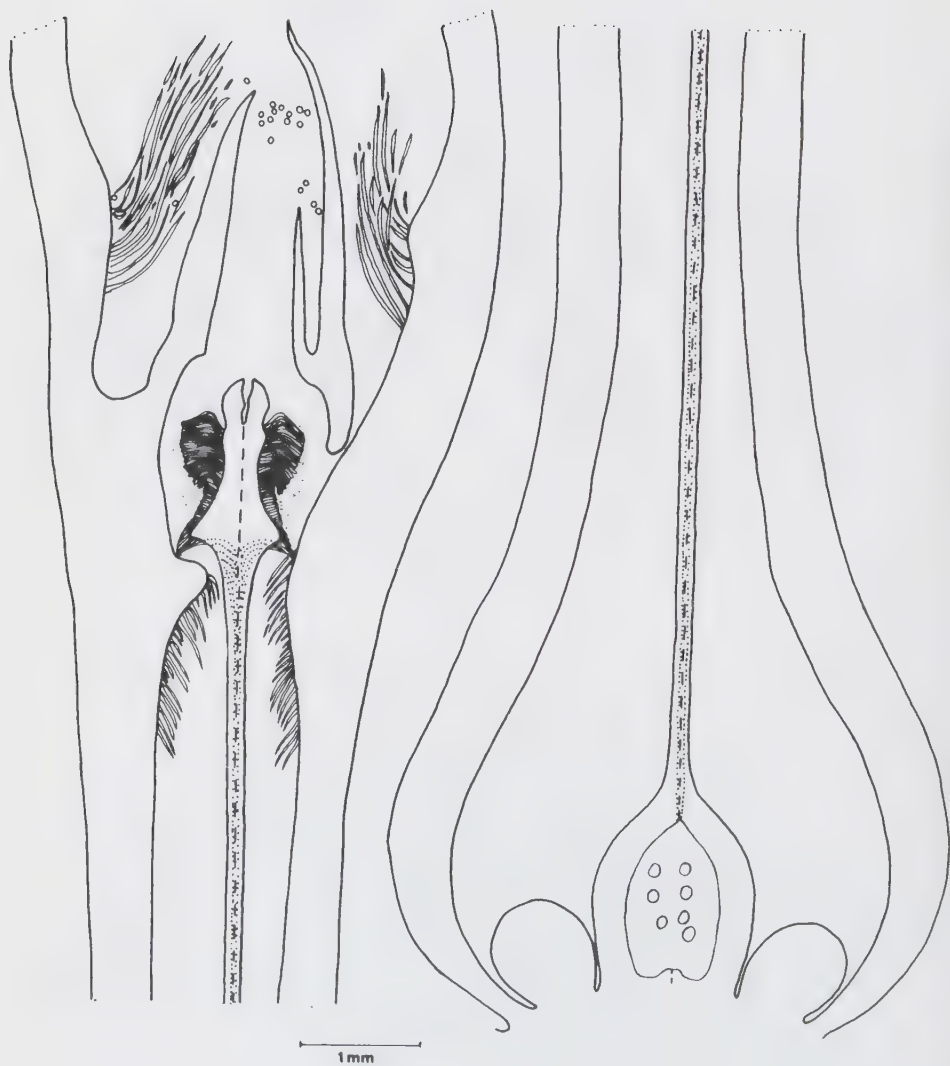
b



16c

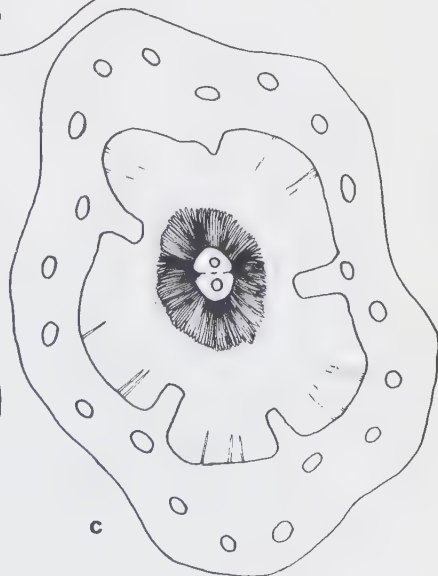


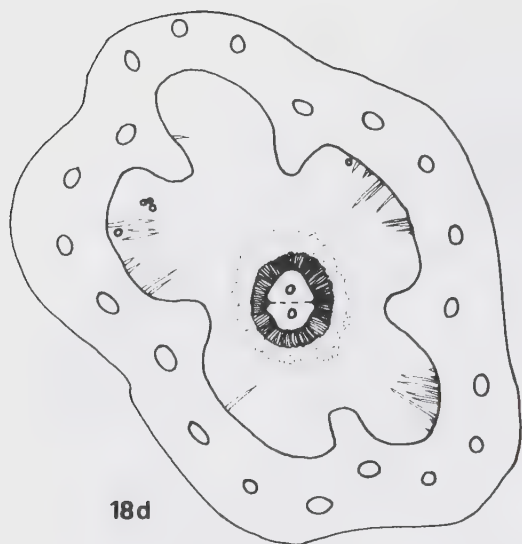
d



18a

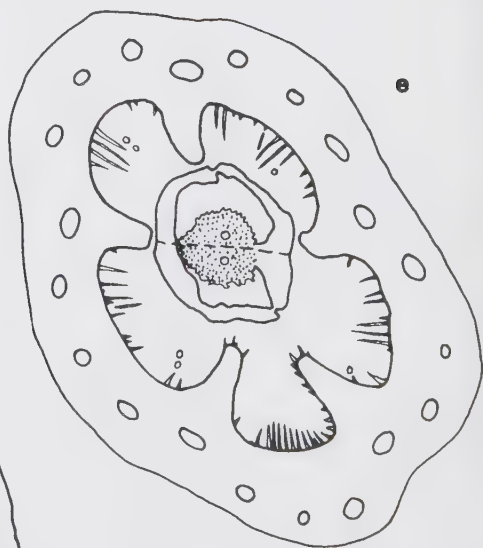
1 mm



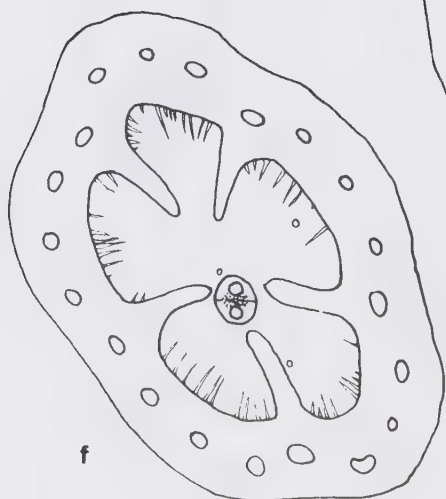


18d

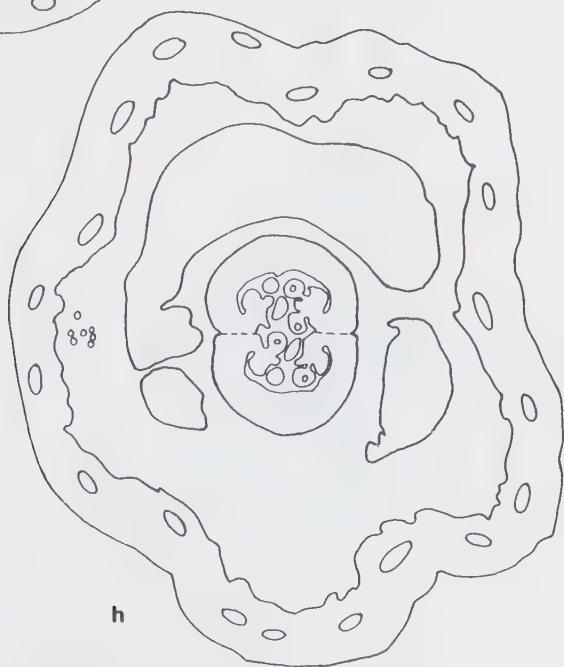
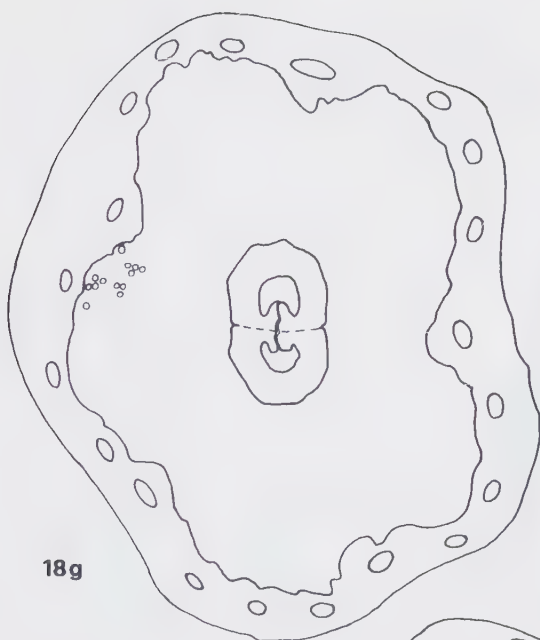
1 mm

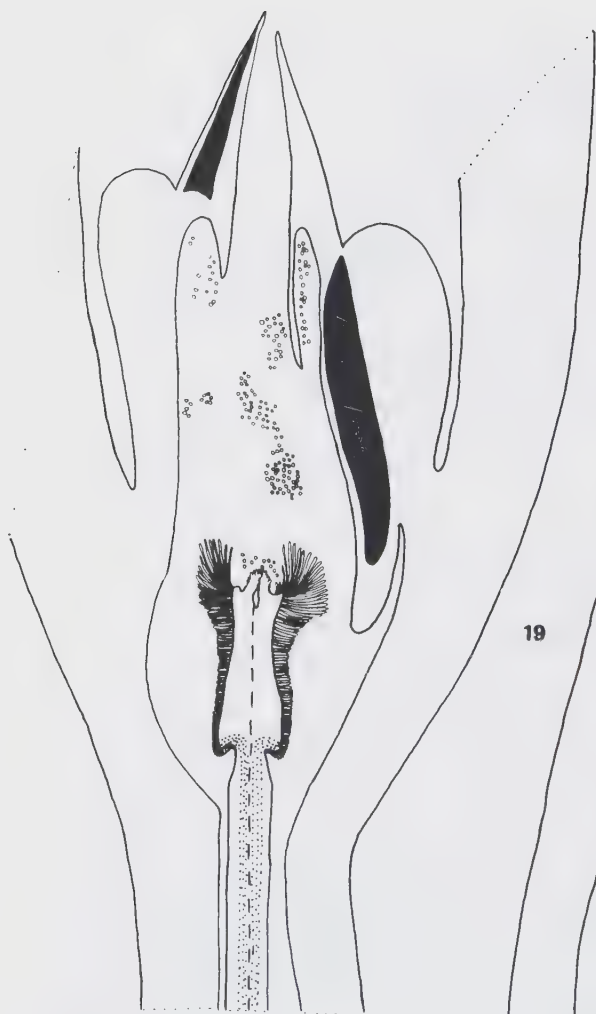


e



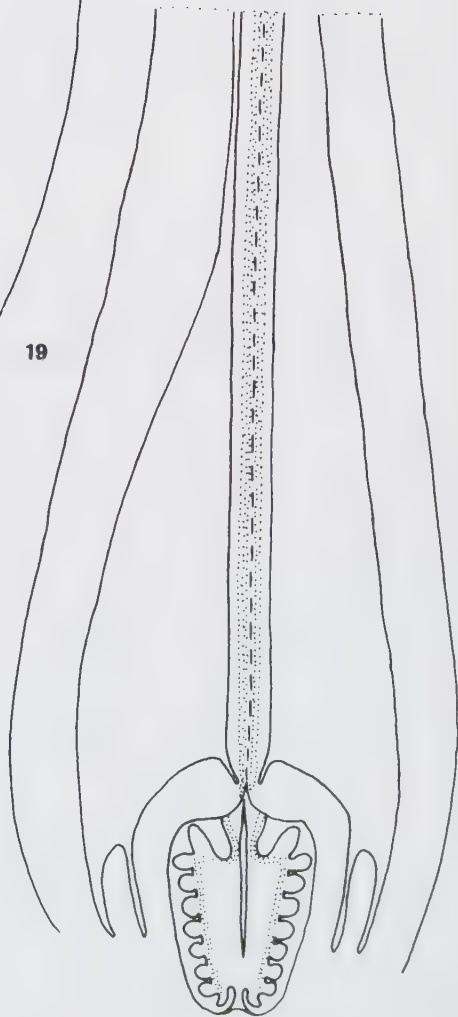
f

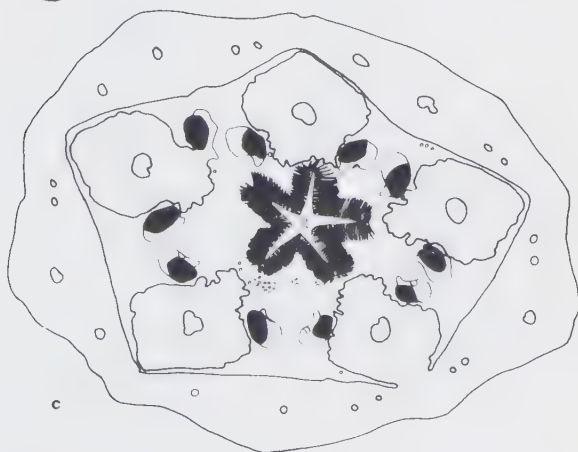
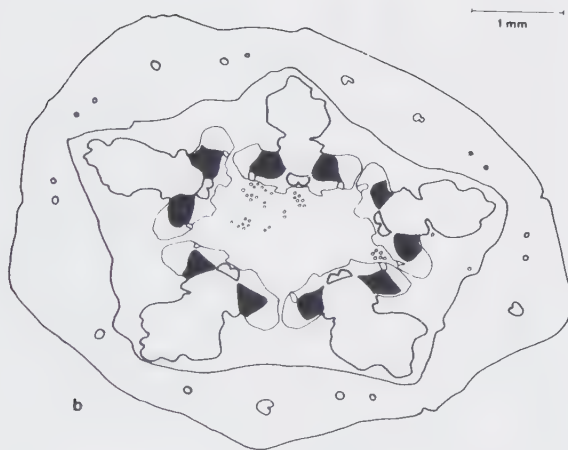
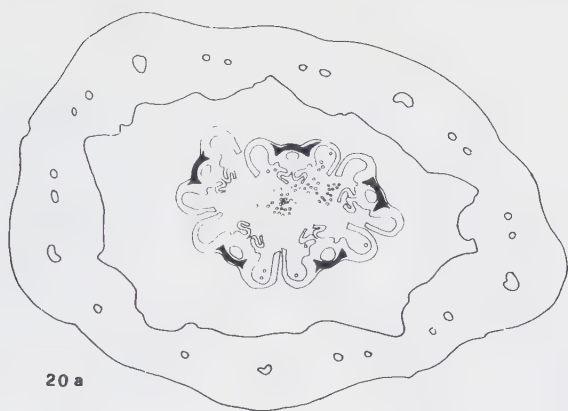


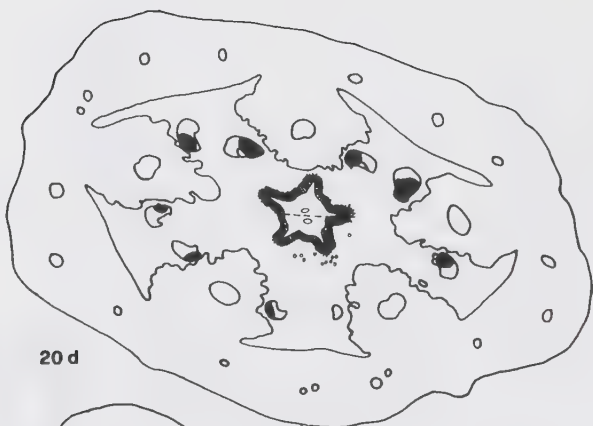


1mm

19



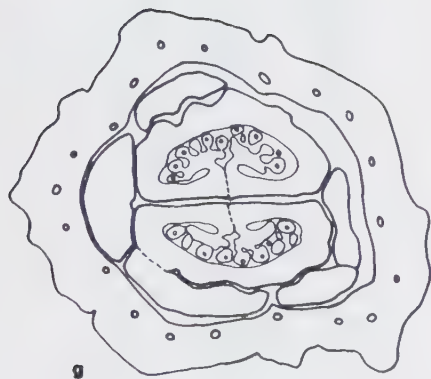
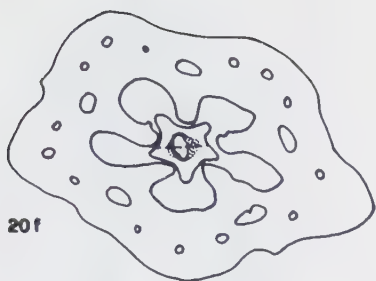




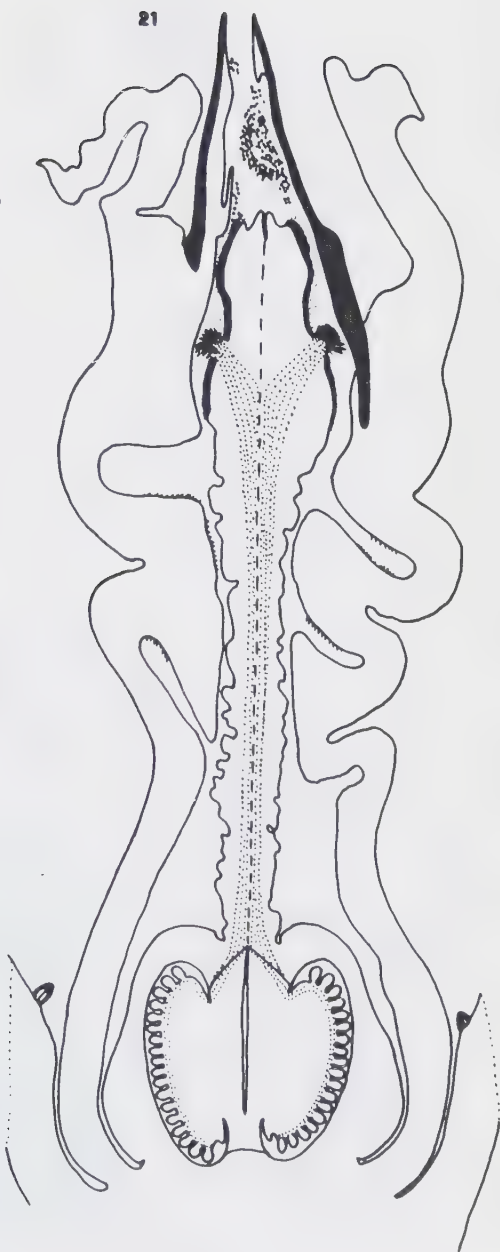
20 d



1 mm

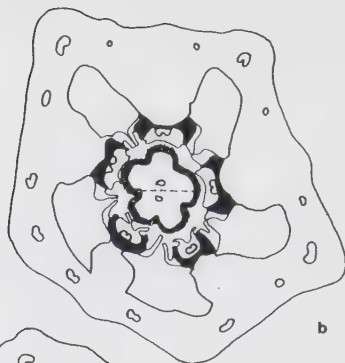


1mm

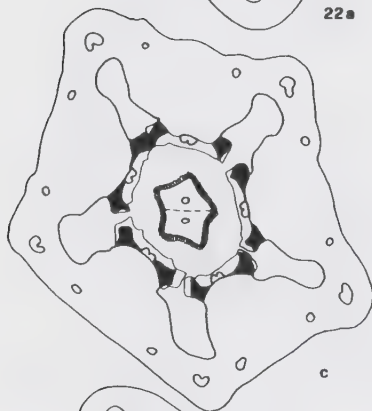




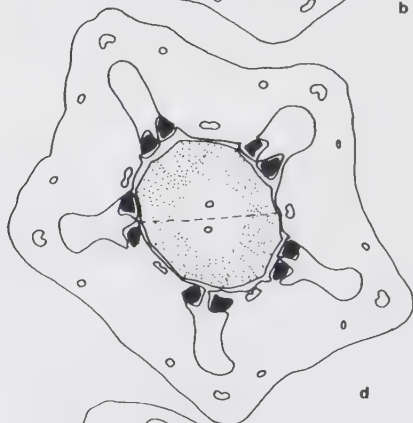
22a



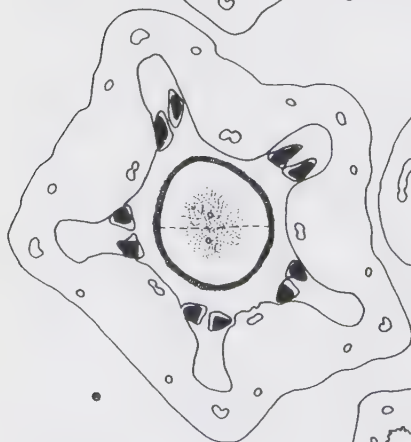
b



c



d



e

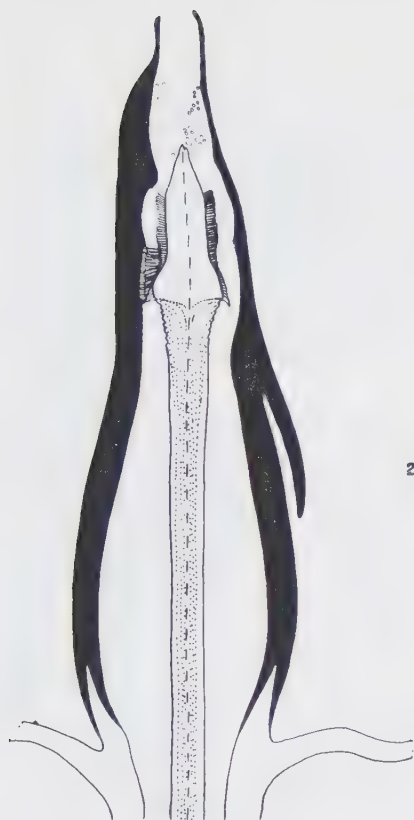


f

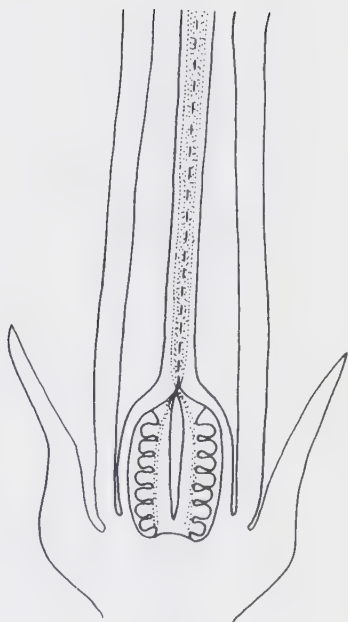


g

1 mm



23



0.5 mm



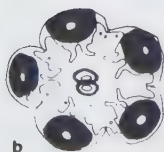
24 a



c



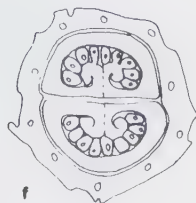
e



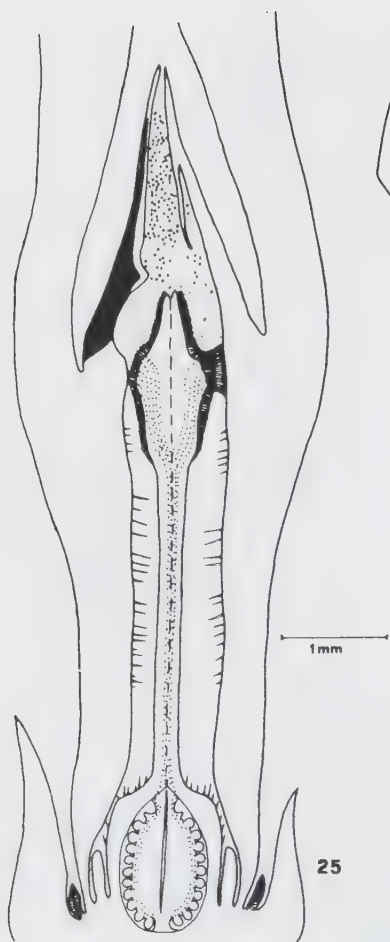
b



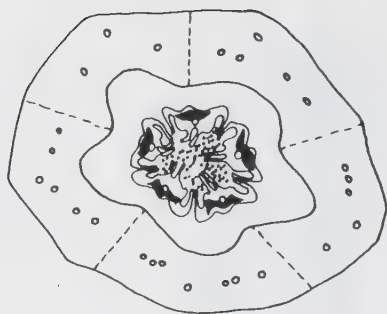
d



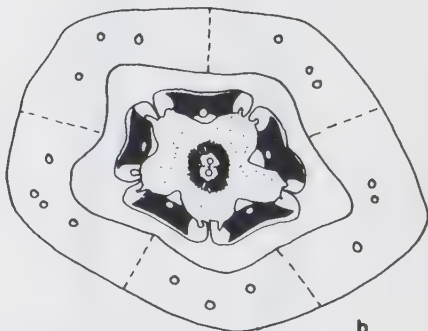
f



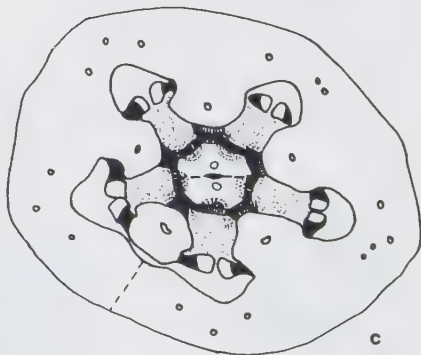
25



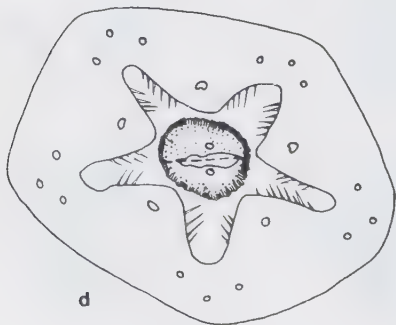
26a



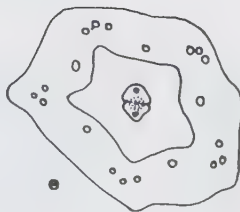
b



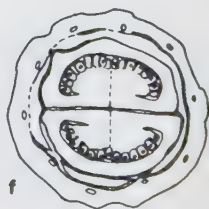
c



d



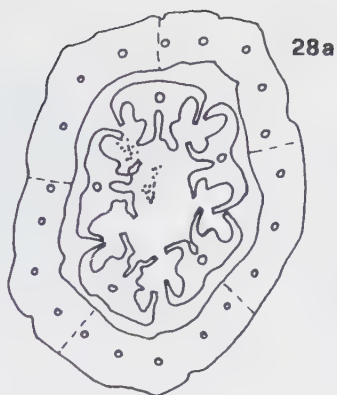
e



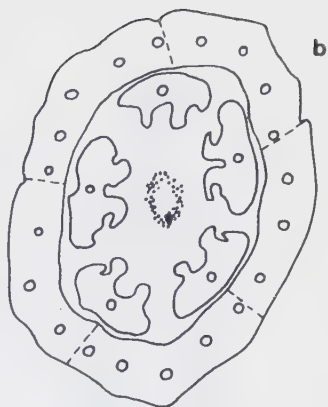
f



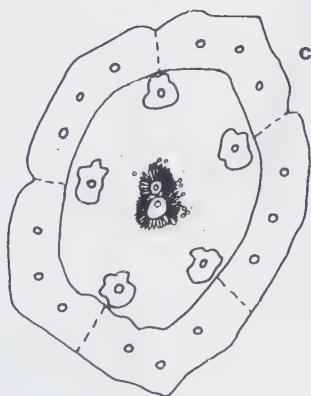
27



28a

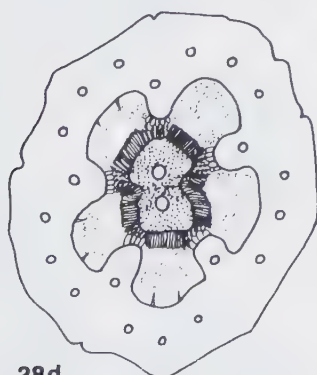


b

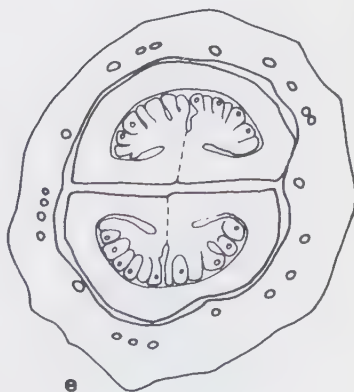


c

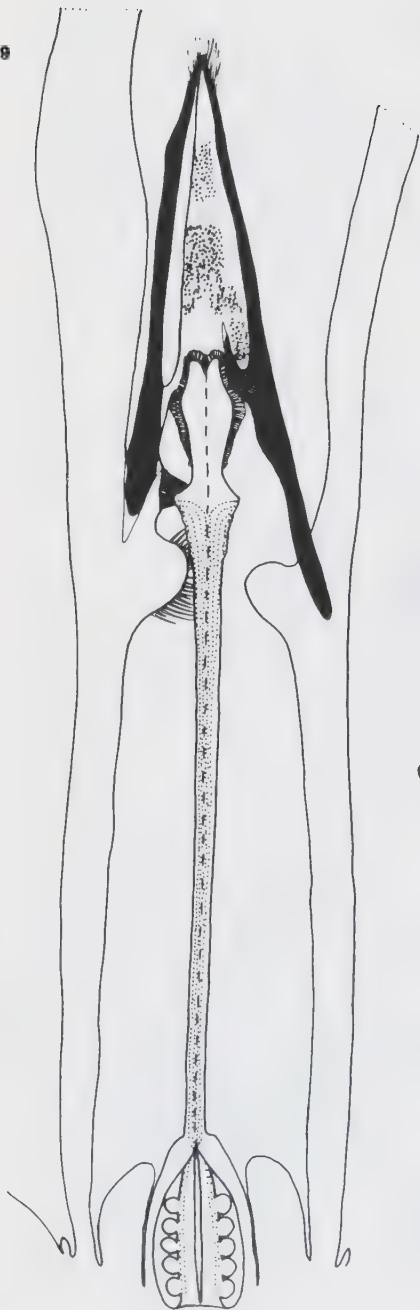
0.5mm



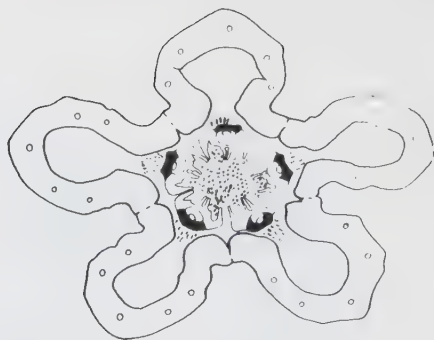
28d



e



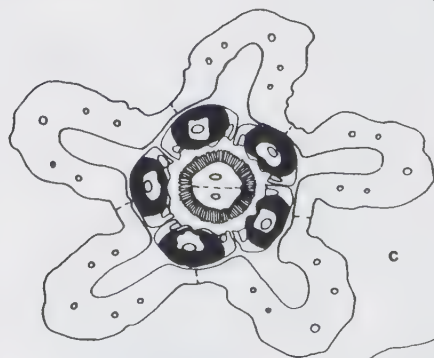
1 mm



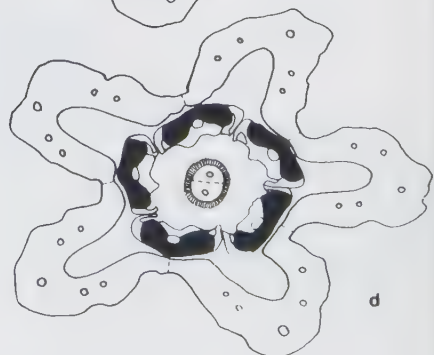
30a



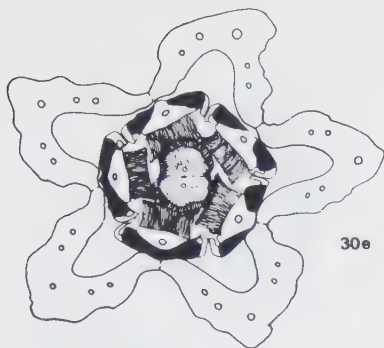
b



c



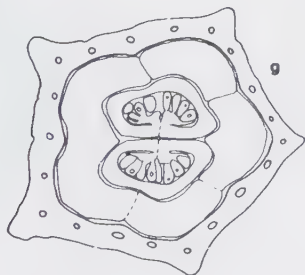
d



30e



f



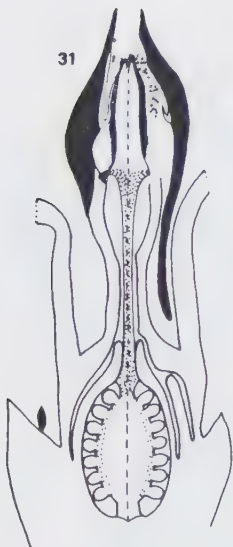
g

30
1mm

31
0.5mm

32
0.5mm

31



32a



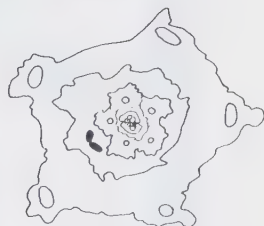
b



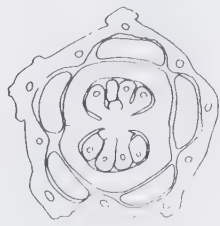
c



d

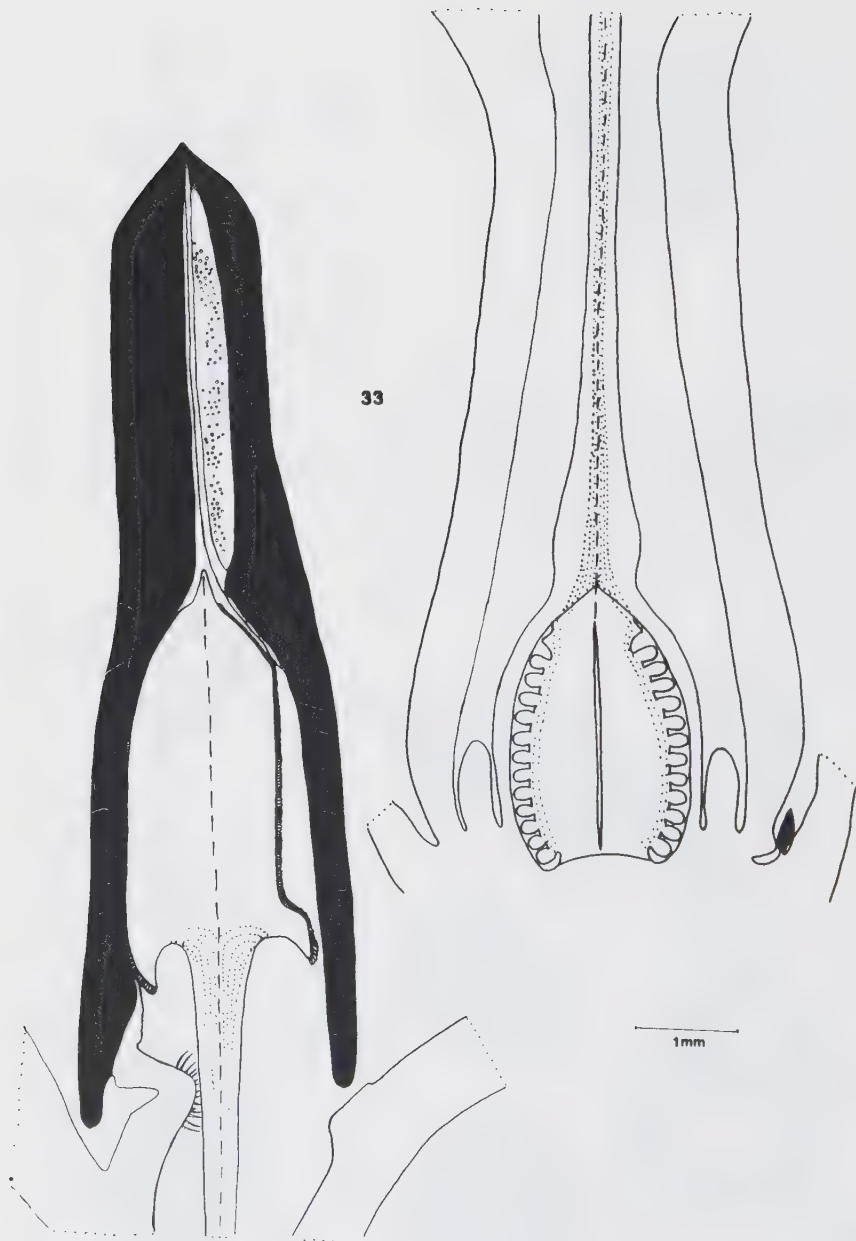


e

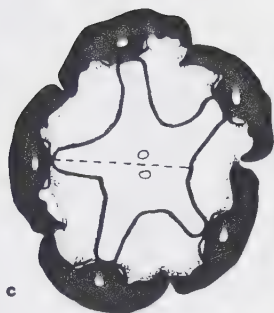
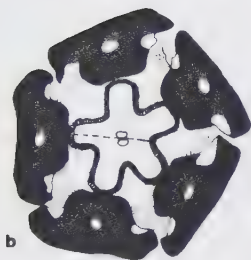


f

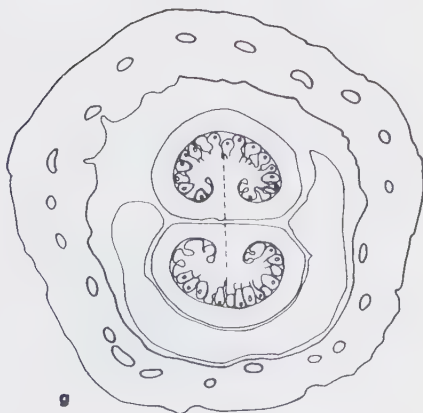
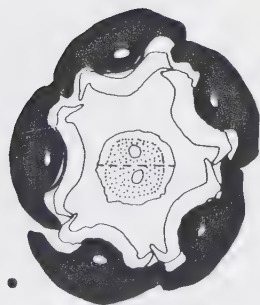
33



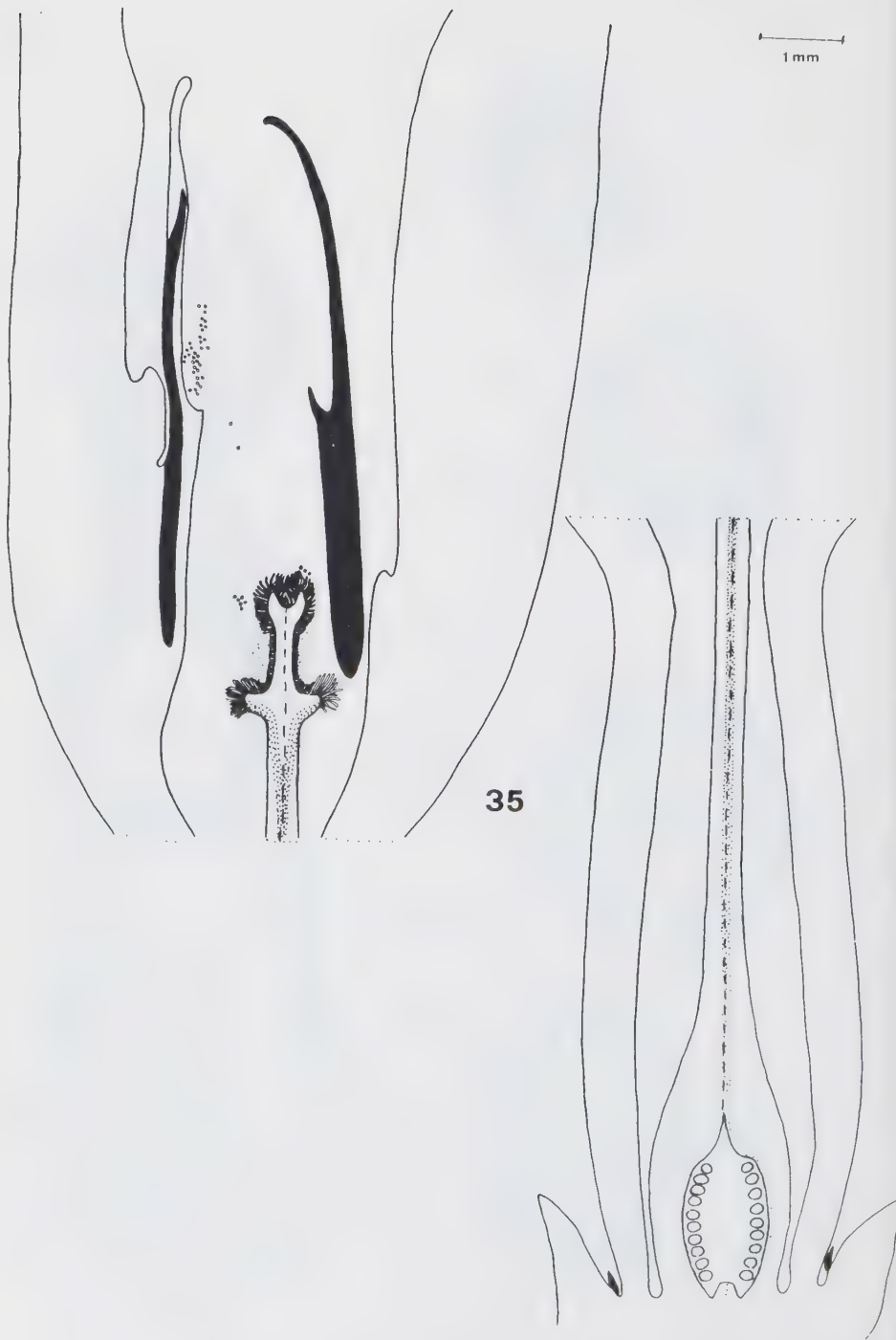
34 ■

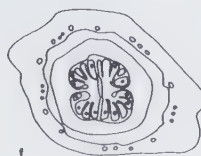
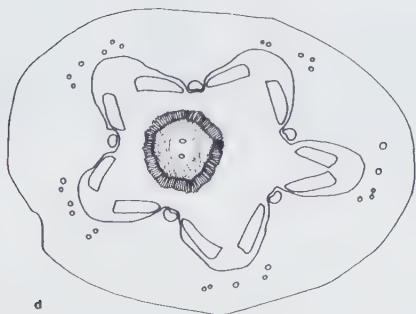
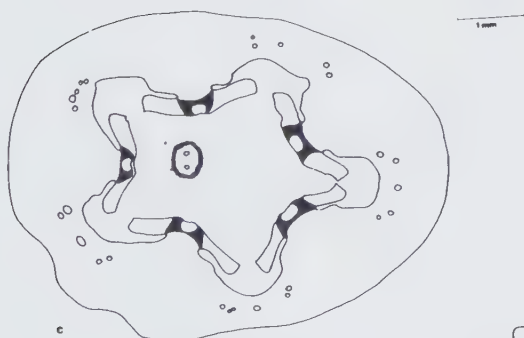
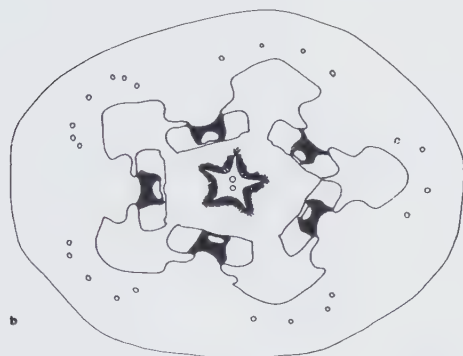
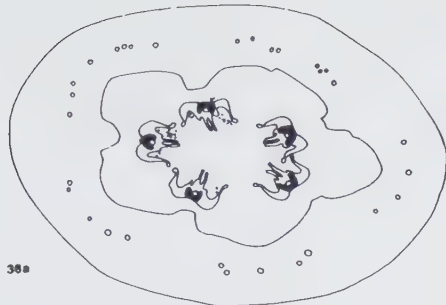


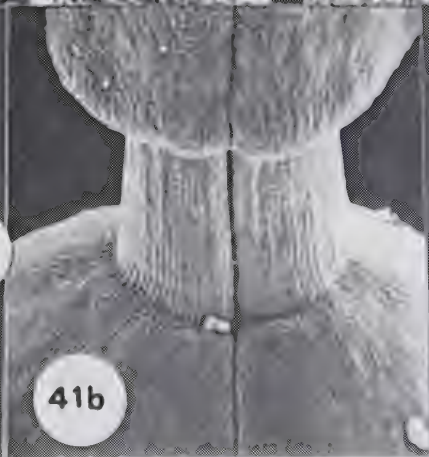
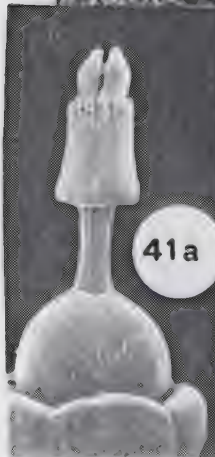
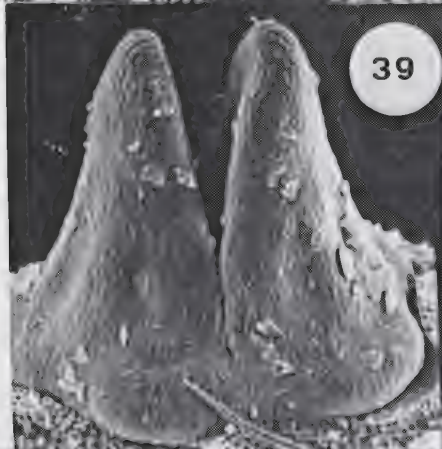
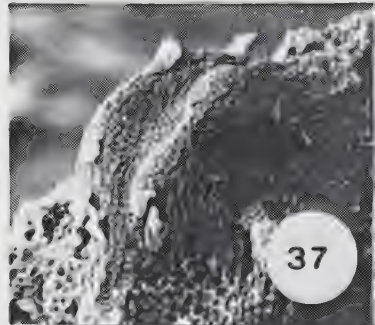
1 mm



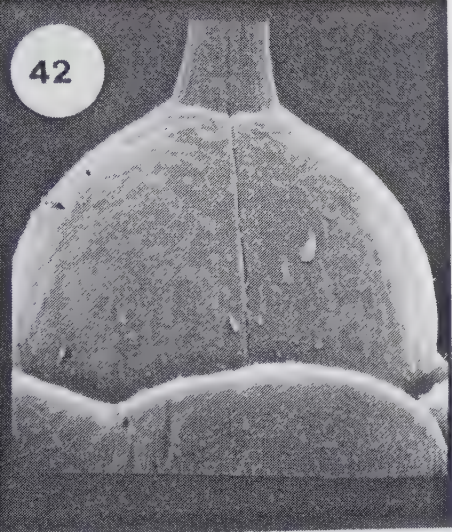
1 mm







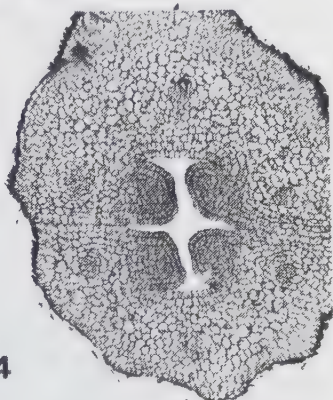
42



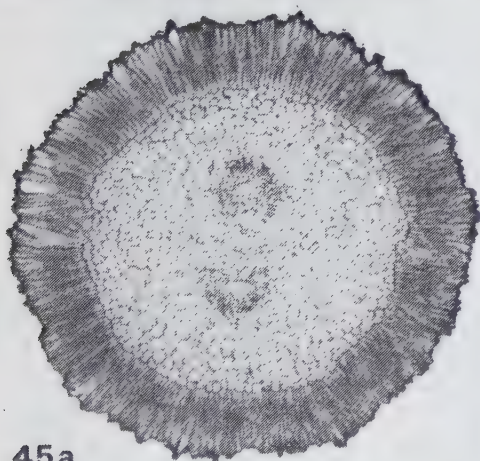
43



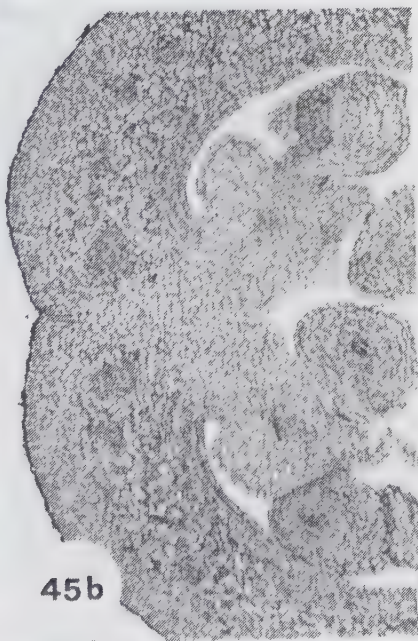
44



45a

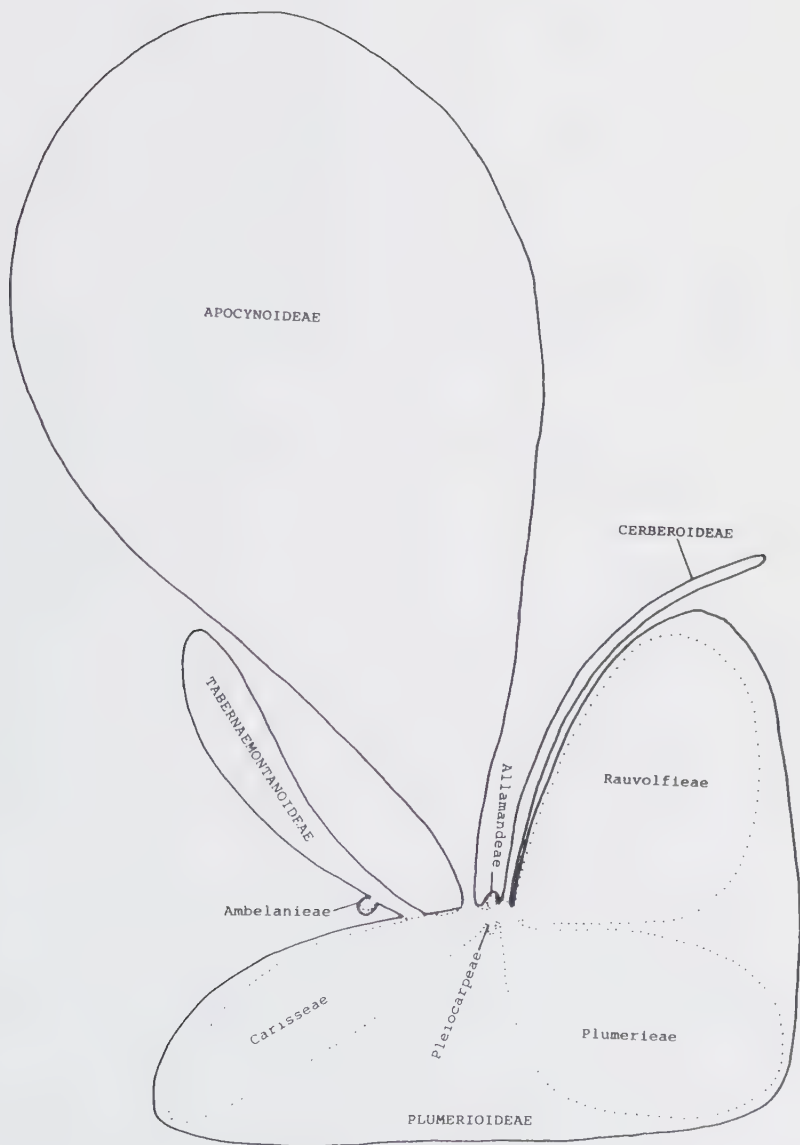


45b



46





CURRICULUM VITAE

von Mary E. Fallen, geboren am 21. April 1949 in Kalifornien, U.S.A.
Heimatort - U.S.A.

- 1956 - 1964 Primar- und Sekundarschule in Petaluma, Kalifornien, U.S.A.
1964 - 1968 Priest River High School, Priest River, Idaho, U.S.A.
Hauptfach: Biologie Zeugnis: Diploma
1975 - 1976 St. Louis Community College, St. Louis, Missouri, U.S.A.
Hauptfach: Biologie
1976 - 1980 University of Missouri, St. Louis, Missouri, U.S.A.
Hauptfach: Biologie/Botanik Zeugnis: B.A.
1980 - 1983 Universität Zürich, Zürich
Hauptfach: Systematische Botanik
1981 Diplom der Philosophischen Fakultät II der Universität
Zürich, Diplomarbeit: "A taxonomic revision of Condylocarpon
(Apocynaceae)." unter der Leitung von Prof. P.K. Endress.
1981 - 1983 Arbeit an der Dissertation unter der Leitung von Prof. P.K.
Endress.

Während des Studiums besuchte ich Vorlesungen und Kurse bei:

C.D.K. Cook
P.K. Endress
K.U. Kramer
E. Landolt
F. Richard
O. Rohweder
E. Thomas
H. Wanner
I. Mendoza-Heuer
E. Urmi
W. Dickison

Früher bestandene Examina: Schlussprüfung in Systematischer Botanik und
Allgemeiner Botanik für das Diplom.

Gegenwärtige Stellung: Assistentin am Institut für Systematische Botanik
der Universität Zürich

